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APPLICATION OF DYNAMIC ENERGY BUDGET THEORY FOR CONSERVATION RELEVANT MODELLING OF BIRD LIFE HISTORIES

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Application of Dynamic Energy Budget theory for conservation relevant modelling of bird life histories

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Cover: Adapted from the lithographic plate developed by John Gould and Henry Constantine Richter, in London, 1864, depicting a pair of House Sparrows (*Passer domesticus*, Ray) at the nest.

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APPLICATION OF DYNAMIC ENERGY BUDGET THEORY FOR CONSERVATION RELEVANT MODELLING OF BIRD LIFE HISTORIES

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Application of Dynamic Energy Budget theory for conservation relevant modelling of bird life histories

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Thesis specifically prepared to obtain the PhD Degrees in

Environmental Engineering and Earth and Life Sciences

Dedicado à minha família
e em particular à Zica,
com muita saudade

Contents

1 Introduction

1.1 The conservation status of birds

Although biodiversity, as a concept, has already been defined by a multitude of authors and agencies, and not always consistently, one possible definition is the one adopted under Article 2 of the United Nations Convention on Biological Diversity, that defines it as "the variability among living organisms from all sources, including, *inter alia*, terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species, and of ecosystems" (UNEP, 1992). Overall, biodiversity includes the variety of life at all levels of organisation, from the level of genetic variation within and among species to the level of variation within and among ecosystems and biomes (Tilman, 1997).

According to the Millennium Ecosystem Assessment (MEA, 2005) between 10% and 50% of well-studied higher taxonomic groups are currently threatened with extinction (based on the IUCN – World Conservation Union criteria for threats of extinction). According to the same report, the distribution of species on Earth is becoming more homogenous and genetic diversity has declined globally, particularly among domesticated species. Worldwide, some 23% of mammals, 32% of amphibians and 25% of conifers are currently threatened with extinction and recent reports have highlighted that vertebrate species populations are, on average, about half the size they were around 1970 (WWF, 2014). The global declining trend observed in terrestrial biodiversity is expected to decline further, with the mean species abundance (MSA) projected to decline from 68% of the level that potential natural vegetation could support in 2010 to about 60% in 2050 (EEA, 2015).

Bird species have been grouped in the biological class Aves, according to Linnaean taxonomy, and in the crown group Neornithes, according to modern phylogenetic taxonomy, and constitute a group species generally considered to have evolved from theropod dinosaurs (Livezey and Zusi, 2007, 2006). Unfortunately and concomitantly with the other vertebrate groups, currently 1,373 bird species worldwide (about 13% of the total) are threatened with extinction. Of these, 213 species are considered critically endangered. The trend is global but it is particularly concentrated in the remaining forested tropical regions. About 80% of the currently threatened bird species have populations that continue to decline and cases of population collapse have also been recently observed (BirdLife, 2014).

The main causes for biodiversity decline worldwide, including those directly connected to human activities, may be generally summed up to: habitat loss, fragmentation and degradation; hunting and fishing (overexploitation); climate change; desertification; waste and pesticide pollution; the introduction of exotic (alien and invasive) species; and disease (CBD, 2014; EEA, 2015; WWF, 2014).

Human activities in general have been pointed out has being responsible for a vast majority of current habitat loss (Bawa and Dayanandan, 1997) and human population density has been shown to correlate with habitat modification (CBD, 2014; Harcourt et al., 2001). These activities often lead to land-use change, which is expected to remain the largest driver of biodiversity loss beyond 2010 and at least to 2050 (CBD, 2014; WWF, 2014).

Globally, the most significant threat for bird species in particular is the conversion of natural habitats to agricultural land, followed by the impact of invasive alien species and other human activities such as hunting, trapping, logging, urban sprawl, pollution and hazardous fishery practices (BirdLife, 2014). The impact of climate change on species, habitats and ecosystems is increasing and it is projected to become progressively more significant during the next decades (EEA, 2015). Several studies have tried to identify possible direct and indirect ways through which climate change may be impacting bird species. Many of these studies rely on climate-envelope modelling. Extinction risks driven by shifts in the abundance and distribution of species in general as climate change forces the colonization of new areas with inadequate ecosystem spatial cohesion or other important traits, have been published since the early years of this century (Thomas et al., 2004; Vos et al., 2008) and continue to be developed for specific groups or regions (Araújo et al., 2013, 2011; Fordham et al., 2013).

Recently, 314 species of birds, corresponding to about half of all the North American bird species, have been estimated to be severely threatened by global warming through expected reductions and shifts in their potential distribution ranges (Langham et al., 2014). But the possible effects of climate change in bird communities are diverse. For instance, changes observed in the communities of birds in the highland forests at Monteverde, Costa Rica, have been attributed to changes in mist frequency (Pounds et al., 1999). Gosler (2002) also associated the 20 years decline in the rate of afternoon fat reserve accumulation in the Great tit (*Parus major*) he has observed with the increase in average daily temperatures. Other studies have been recording changes in body size for several bird species and frequently associate these changes with global warming. Yom-Tov et al. (2006) observed decreases in body weight and increases in wing length in 14 species of passerine birds at two localities in England and associated these changes with the increase in average temperatures, referring to the Bergmann's and Allen's rules, respectively. Some years later, van Buskirk et al. (2010) reported that migrating birds captured at a banding station in western Pennsylvania, USA, have exhibited steadily decreasing fat-free mass and wing chord since 1961, and interpreted these observations as consistent responses to a warming climate. Contrasting with these studies, Goodman et al. (2012) observed an increase in the wing length and body mass of bird species from two long-term banding data sets from central California that spanned 40 and 27 years respectively. These authors proposed the effect of changes in food availability and primary productivity. Other recent studies have also supported the hypothesis of changing food availability driving changes in body size (Yom-Tov and Geffen, 2011).

It is clear that there is substantial uncertainty regarding the direct and indirect ways through which climate change may be affecting bird species. In this context, some authors have highlighted the utility of theoretical models in order to relate body size to metabolism, to understand the proximate mechanisms and consequences of size shifts and to assess the vulnerability of species under the effect of climate change (Gardner et al., 2011; Martin, 2004; Monaghan and Nager, 1997).

There is also a broad consensus that in the absence of conservation action, biodiversity will continue to be lost at a rate unprecedented in the recent era (Gregory et al., 2005). Considering that many aspects of the stability, functioning, and sustainability of ecosystems depend on biodiversity, then its loss will lead to a deterioration of ecosystem services, increasing the likelihood of ecological unexpected events with negative impacts on human well-being (MEA, 2005).

Taking all of this into consideration, developing the study of the metabolism and the physiology of as many organisms as possible, including those belonging to highly threatened

vertebrate groups, and integrating these into explicit models that may serve the purposes of successful conservation is paramount.

The most recent efforts to advance knowledge on physiology for conservation purposes have been summarized under the term 'conservation physiology' (Cooke et al., 2013), but most of the work has been focused on thermoregulatory abilities, particularly in the context of climate change (Seebacher and Franklin, 2012) or on stress related hormonal and immune responses (Ellis et al., 2012).

The mechanisms of energy intake, assimilation, allocation and use haven't been so frequently explored and modelled for conservation purposes. On the one hand, this has been attributed to the complexity of physiological mechanisms underlying life history trade-offs and particularly to the extra difficulty of describing and measuring metabolism, metabolic processes and energy budgets (Zera and Harshman, 2001). On the other hand, this situation is also probably due to the way the study of life history evolution in general and avian life history evolution in particular, progressed through the years. In fact, when we consider the study of life history evolution we are able to observe how the focus on the effects of possible exogenous drivers of variation and their respective consequences in terms of fitness and reproduction, dominated most of the research produced.

However, some efforts to integrate mechanistic approaches to physiology and metabolism into the study of life history evolution did occur. The next section will review these developments.

1.2 The study of avian life history evolution

The study on the life history of organisms and the evolution of life history strategies can easily be traced back to the beginning of the 20th century (Kunstler, 1900). Fisher (1930) published one of the first landmark studies aiming to describe the drivers and the processes of life history evolutionary change, exploring the genetic implications of natural selection.

Life history theory has been mainly focused on reproductive success and the concept of 'fitness'. Reproduction costs were among the first indicators to be adopted (Moreau, 1944). These have been expressed through clutch size (Lindén and Møller, 1989), quality and size of hatchlings (Filin, 2015; Styrsky et al., 2000) or parental survival and senescence (Boonekamp et al., 2014; Dijkstra et al., 1990). The diversity in life histories have also been studied through the analyses of population dynamics and survival rates (Cole, 1954; Lindström, 1999).

Two fields of research have been particularly explored, aiming at the identification and characterization of: a) global patterns and b) drivers of variation. Gadgil & Bossert (1970) elaborated on the adaptive nature of life histories to explain the existence of patterns and since then other authors described patterns across different latitudes, geographical elements and climates (Olson et al., 2009). Concerning the factors driving life history evolution, these have been generally classified as exogenous (environmental) or endogenous (e.g., genetic).

The different exogenous drivers explored in literature include resource availability (Lack, 1968; Martin, 1987), sibling competition (Royle et al., 1999), predation pressure (Martin, 1993), territoriality (Newton, 2003), population dynamics (Paladino, 1989) or taxonomic turnover (Olson et al., 2009). The effects of these drivers assessed through reproduction costs or stress indicators and their covariation with life history traits have been occasionally reviewed (Ellis et al., 2012; Lindén and Møller, 1989).

Stearns (1976) was one of the first authors to point out that specific combinations of life history traits would occur in particular sets of circumstances and recently Dobson (2012) referred to the cases of hummingbirds and petrels, which have different body sizes, diets and habitats, but exhibit similarly low reproductive rates as examples illustrating that different combinations of life history traits could lead to similar life history patterns (the "lifestyle hypothesis").

Studies searching for endogenous drivers of life history variation have been mostly focused on phylogeny and the influence of phylogenetic inertia (Padian and Chiappe, 1998). For instance, Sibly *et al.* (2012) concluded that strong phylogenetic signals may have lead to the conservation of similar life history traits within clades and Pienaar *et al.* (2013) observed that the evolution of body and egg mass or the duration of the incubation and fledging periods seem to be affected by strong phylogenetic inertia. Other endogenous drivers that have been explored in previous studies deal mostly with genetics. These include the expression of genetic variance through different levels of heritability (Husby et al., 2011) or the phylogenetic implications of molecular variation (Hackett et al., 2008; Zhang et al., 2014).

The existence of relevant processes taking place at the physiological and metabolic scales has been harder to study. Notwithstanding, many authors have been highlighting the need to deepen our knowledge about the way avian physiology determines the life history traits we observe today. For instance, Partridge & Harvey (1988) highlighted the need to identify the physiological processes that enable the phenotypic plasticity of organisms. Some years later, Monaghan & Nager (1997) identified the lack of a comprehensive account of all the costs associated to reproduction besides those dealing directly with rearing the hatchling and called for research on the existence of proximate mechanisms and physiological constraints. Half a decade later, Zera & Harshman (2001) reviewed the physiology of life history trade-offs and suggested that the concept of a physiological trade-off implies a negative functional interaction, stressing the need for research on the physiological costs and constraints associated with life history traits. In his review on the evolution of avian life histories, Martin (2004) also presented several hypotheses regarding the existence of proximate mechanisms of variation in trait expression, mediating the effect of environmental selective pressures on life history traits.

Previous attempts to account for the metabolic costs associated with different life history traits focused on reproduction costs for the progenitors (Roby and Ricklefs, 1986; Trillmich, 1986; Ward, 1996), their respective general metabolic rates (Thomson et al., 1998) or the implications for nestling development (Drent and Daan, 1980; King, 1973; Ricklefs, 1974). Other studies focused on indirect effects such as the possible trade-offs between reproduction and assimilation, growth, and thermoregulation (Karasov, 1986; Konarzewski, 1995; Weiner, 1992), immunocompetence (Hanssen et al., 2005; Owens and Wilson, 1999) or plumage coloration and signalling (Doutrelant et al., 2012).

The development of models has included theoretical and experimental approaches. Early models attempted to describe the costs and profits of growth, maintenance and reproduction through specific functions (Gadgil and Bossert, 1970) and recent models include biophysical experimentation (usually assuming a conservation perspective) (Kearney, 2012; Pennisi, 2012).

The importance of developing more explicit, mechanistic and individual-based models linking the constraints of metabolism to life history traits has been frequently highlighted in order to: a) understand the evolution of life history strategies (Lindström, 1999; Zera and Harshman,

2001); b) improve our future conservation strategies (Seebacher and Franklin, 2012); and c) to create general ecosystem models (GEM) (Harfoot et al., 2014; Purves et al., 2013).

In this context, the study of avian metabolism and energetics emerges as a field that, despite the occasional interaction with the study of avian life history evolution and more recently with conservation science, had its own development and may still deliver substantial contributions for these matters, particularly through explicit, mechanistic models. Taking this into consideration, in the next section we will summarize these useful contributions.

1.3 The study of avian metabolism and energetics

The modern study of metabolism and energetics in animal species has a long history with some authors pointing out the interest manifested by Da Vinci in the 15th century (Fort et al., 2011) and the experiments of Lavoisier and Laplace in 1783 (Blaxter, 1989), as its fundamental beginning. The development of thermodynamics as a scientific discipline in the 18th and 19th centuries (Gibbs, 1876; Joule, 1884; von Helmholtz, 1882) was particularly important as it led to the study of biological thermodynamics in the 20th century, both in the laboratory (Krebs and Kornberg, 1957) and in the field (Schmidt-Nielsen, 1998, 1972). The measurement of an increasing diversity of characteristics on a larger number of species have since been possible due to the continuous advancement of technology and miniaturisation (Fort et al., 2011; Kearney, 2012; Ropert-Coudert and Wilson, 2005). Nevertheless, metabolism and the energy exchange that organisms establish between themselves and the surrounding environment, in order to build and maintain their structure and reproduce, have actually been studied in a very small number of animal species considering the total number of currently known species. The determination of resting metabolic rates (RMR), for instance, has only been performed for some hundreds of bird species within a universe of about 10,500 currently known species (Bennett and Harvey, 1987; Blaxter, 1989; Glazier, 2008).

The study and modelling of animal metabolism is useful for many reasons. This becomes clear when we consider that the abundance, distribution and life history of species are partially determined and constrained by the metabolic processes taking place in dynamic environments, particularly in terms of temperature and resources such as food availability (Andrewartha and Birch, 1954; Kearney, 2012). Therefore, assuming an ecological perspective, these studies may be useful to investigate the niche represented by certain environmental and resource conditions (Araújo et al., 2013; Kearney, 2012). Considering the standard use of the same energetic units (e.g., Joules, J), they may also be useful for comparative purposes across the organizational (Ernest and Brown, 2001; Harte, 2011), spatial (Davies et al., 2007; Root, 1988) and temporal scales (Brown and Adams, 1984; McWilliams et al., 2004).

Studying the energetics of birds in particular is also useful for a diverse number of reasons. On a general level, it allows for a better understanding of how the energy balance is maintained throughout the life cycle of individuals and how much this balance is determined by processes such as growth, maturation, feeding and reproduction. On other more specific levels, several reasons can be identified.

From a physiological perspective, the study of avian energetics is useful to explore the metabolic constraints to the embrionary development (Starck and Ricklefs, 1998a; Vleck and Vleck, 1987) or the post-hatching growth of birds (Bourdon et al., 2009; Starck and Ricklefs, 1998b; Teixeira et al., 2014) as well as to understand the relationship between metabolism and specific functions such as those related to thermoregulation (Nilsson et al., 2011; Ruben, 1995),

the endocrine system (McNabb et al., 1998) or immunocompetence (Apanius, 1998; Owens and Wilson, 1999).

From an evolutionary perspective, these studies may provide a better understanding of how natural selection, driven by exogenous and endogenous pressures, including energy balance optimisation, has influenced the evolution of life history strategies (Gadgil and Bossert, 1970; Maury and Poggiale, 2013; Pienaar et al., 2013) and the phenotypic plasticity we observe today (Partridge and Harvey, 1988; Rezende et al., 2004). They may also enable a better comprehension of how trade-offs between different life history traits may have evolved (Martin, 2004; Zera and Harshman, 2001).

From an ecological perspective, these studies may help to assess how different strategies are employed by birds in order to optimise their energy budgets in different kinds of habitats (Fort et al., 2011; Le Maho, 2002; Maclean, 1996) or how different lifestyles may be associated with similar life history patterns (Dobson, 2012). They may also enable the quantification of food requirements for birds and clarify the role of birds as prey (Brown et al., 2004; Fort et al., 2011; Kooijman, 2010a; Teixeira et al., 2014).

From a taxonomic perspective, studies on the energetics of birds may contribute to harmonize different approaches such as those primarily relying on molecular (Hackett et al., 2008; Zhang et al., 2014) or morphological (Livezey and Zusi, 2007, 2006) characteristics. This way, such studies may also contribute to the debate regarding the origin and evolution of birds (Feduccia, 2002; Feduccia et al., 2005; Padian and Chiappe, 1998; Prum, 2003; Sereno, 1999; Zhou, 2004), potentially helping to solve such controversies as those about the placement and evolutionary relevance of *Archaeopteryx* (Lee and Worthy, 2011; Ostrom, 1976; Xu et al., 2011).

Finally, from the conservation perspective, studying the energetics of birds may enhance their use as ecological indicators considering their frequent position at the apex of trophic networks (Fort et al., 2011). Within the scope of conservation physiology (Cooke et al., 2013), detailed knowledge of avian metabolism may facilitate the establishment of indices of physiological stress and condition, allowing for better estimates on species persistence under different scenarios (e.g. land-use change, climate change and food-web disturbance) at all scales (Einoder, 2009; Ellis et al., 2012; Fort et al., 2011; Seebacher and Franklin, 2012).

On a very practical level, studies on the energetics of birds may also contribute to fill in the gaps of knowledge regarding a large number of poorly documented species. Models used to estimate the maximum population growth rate such as that developed by Cole (Cole, 1954) require values of fecundity and mortality rates. These rates require information on life history traits such as the age at first breeding or clutch size, among others. However, even for the most studied animal groups, such as the birds, there is a considerable amount of information lacking. In this regard, reliable data estimates are required in order to fill in the gaps and model the effects of global change for instance, in an optimized amount of time.

1.4 The techniques used for the study and modelling of energy in birds

There is a diverse number of approaches and techniques currently in use for the study and modelling of energy in birds (Fort et al., 2011). Some of these approaches rely mostly on experimental procedures while others are fundamentally theoretical. The first kind is also often complemented with some theory for the purpose of converting mass or other

physiological data, such as oxygen consumption, to energy. In terms of the experimental procedures used these may include individual weighing of individual birds (Grémillet et al., 2000, 1996; Spée et al., 2011), the administration and measurement of isotopes using the doubly-labelled water (DLW) (Harding et al., 2009; Shaffer, 2011; Speakman, 1997) or the ^{13}C labelled bicarbonate (Fort et al., 2011; Hambly and Voigt, 2011; Hambly et al., 2004, 2002) procedures, heart-rate recordings (Bevan et al., 1994; Green, 2011) and the overall dynamic body acceleration measurement using accelerometers (Halsey et al., 2011; Wilson et al., 2006).

Theoretical approaches have been developed mostly due to the fact that for many species a very limited amount of information or no information at all, is available. The most common theoretical approach is probably the use of allometry. Allometric scaling relationships have been studied and used for almost two centuries since the first considerations relating surface area and metabolic rates were presented (Sarrus and Rameaux, 1836). These studies have been focused on a variety of bird species, usually involving the scaling of body mass with other traits (Lislevand et al., 2007) including the Basal Metabolic Rate (BMR) (Brody and Proctor, 1932; Glazier, 2008; Hulbert and Else, 2004; Lindström and Kvist, 1995; Scott et al., 1996; White, 2011). For this purpose allometry studies usually need previous measurements of energy requirements or metabolic rates and body mass values for a number of species. The history, advantages and constraints of allometry have been frequently reviewed in literature (White, 2011). Among the diverse number of known constraints to the use of allometric scaling relationships of an exclusively mathematical nature is the fact that these assume similarities between species based mostly on body mass, ignoring dimensional differences and the consequences that arise from these, and therefore are highly sensitive to the inclusion or exclusion of particular groups of organisms (Lynch and Fagan, 2009).

Finally it has been increasingly common to use theoretical modelling based on simple mechanistic rules to describe how species take up and use energy and mass. Models that can be applied to a wide range of species have been developed, enabling estimations to be made on the state of pools and flows of energy and mass in populations, communities and ecosystems. These models may ultimately lead to the establishment of theories in ecology if currently recognized inconsistencies are addressed (van der Meer, 2006). Within this approach, thermodynamic modelling has been used when very limited or no information is available besides some morphological properties of the species. This approach uses the first principles of thermodynamics to perform theoretical calculations upon the energy requirements of species, considering a given shape, mass, and other life history traits (Fort et al., 2011, 2009). Static Energy Budgets (SEB) have been particularly popular. These studies try to capture a snapshot of the energy fluxes for an individual in a given state, frequently compiling the measurements of the energetic costs of specific activities per unit of time and then using detailed time budgets (stipulating the duration of each activity) to programme time-energy budgets and estimate the energy requirements of the species (Goldstein, 1988; Grémillet et al., 2005, 1995; Harding et al., 2009; Jürgens and Prothero, 1991; MacMillen and Carpenter, 1977). However, SEB models do not quantify the overhead costs of growth and assimilation and do not account for maturation and reproduction costs besides maintenance which is usually accounted indirectly through respiration (the uptake of dioxygen or the production of carbon dioxide and/or heat) (Kooijman, 2012). Alternatively, Dynamic Energy Budgets (DEB) follow how energy fluxes change during the life cycle of organisms. Currently, the DEB theory (Kooijman, 2010a, 2000, 1993, 1986; Kooijman et al., 2008; Sousa et al., 2010, 2008) is the only metabolic theory that makes use of these models and complies with the laws of thermodynamics.

1.5 The Dynamic Energy Budget (DEB) theory

The DEB theory is a metabolic theory that complies with the laws of thermodynamics, unifying traits that are common to all organisms and linking different levels of biological organisation (cells, organisms and populations) (Kooijman, 2010a; Kooijman et al., 2008). The theory uses simple quantitative and mechanistic rules that describe the uptake and use of energy and nutrients (substrates, food, light), the organisation of metabolism and the consequences for physiological organisation throughout the life cycle of organisms (Sousa et al., 2010, 2008).

Using the DEB theory, the difference between species can be reduced to differences in a single set of parameter values. Some of these parameters represent metabolic processes that are not easily measured but may correspond to the proximate mechanisms that mediate the effect of environmental selective pressures on life history traits as well as to the physiological constraints that determine the way organisms respond to change at the individual or evolutionary scales. Particularly relevant are those parameters defining priority rules in the allocation of energy to different metabolic processes.

Building upon a set of concrete cornerstones, the DEB theory can also explain many general observations, such as the body size scaling relationships of certain physiological traits (Kooijman, 2010a). The DEB theory requires a certain level of abstraction as the state variables and model parameters are not directly measurable. Similarly to SEB models, these need to be estimated from previously collected data.

The application of DEB theory has allowed for very detailed work in a wide range of species, covering almost all larger animal phyla and all chordate classes (Kooijman, 2013; van der Meer et al., 2014), progressively being compiled in the "Add_my_pet" library (Kooijman, 2014a). Some insights have been obtained considering this wide range of species (Kooijman, 2014b, 2013) and some studies focused on groups of species in particular, such as insects (Maino and Kearney, 2014) or marine organisms in general (Sarà et al., 2014).

The standard DEB model describes the ontogeny of an organism through the dynamics of three state variables – structure ($V = L^3$), reserve (E) and maturity (E_H) – using a set of 'primary' and 'compound' parameters. Primary parameters are connected to a single underlying process and compound parameters are simple functions of parameters, typically depending on several underlying processes.

DEB parameters can also be classified as 'core' or 'auxiliary'. Core parameters are linked to underlying assumptions of DEB theory and relate directly to processes that control the state variable dynamics, which are of an abstract nature. Auxiliary parameters link these abstract variables to quantities that can be measured directly (e.g., length, weight, respiration, etc).

Finally, DEB parameters can also be classified as 'intensive' or 'design' according to their physical meaning and relationship with body size. Intensive parameters are independent of body size. Design parameters co-variate with structural body length. The appropriate ratios of design parameters can also be intensive.

In DEB theory the use of scaling relationships includes body size as a result of underlying processes and not as an independent variable with which eco-physiological properties are regressed empirically (as in allometric relationships). Allometry is not used in DEB theory but physiological quantities (e.g., body weight) and processes (e.g., respiration) are functions of parameters. Inter-species comparisons are performed using the 'zoom factor' – the ratio

between each species maximum structural body length and that one of a reference species (which may generally be equal to 1 cm). The maximum structural body length is a compound parameter in itself, calculated from other parameters. Several primary and secondary scaling relationships rely on the way DEB primary and compound parameters relate to structural length and therefore theoretical expectations emerge whenever we compare species with differences in length.

1.6 General goal of the dissertation

The present thesis aims at providing a useful contribution to our knowledge regarding modern birds (the Neornithes) as a group.

Extensive research has been developed throughout the last century on many aspects of the life history of birds. A considerable amount of studies have been focused on the ecology of birds, their remarkable diversity of phenotypes and life history traits and their behaviour. Another considerable group of studies, mostly of an experimental nature, have advanced our knowledge regarding the physiology and metabolism of birds. Particularly during the last few decades, a diverse number of other studies and reports have been focused on the conservation of birds, exploring the causes that led to previous extinctions and the causes that currently drive the decline of biodiversity worldwide. Scenarios of global change, particularly addressing land-use and climate change, have been drawn and the chances of adaptation have been estimated for a fraction of the total number of bird species living today, mostly through the application of statistical and climate envelope modelling techniques.

Some researchers have attempted to link conservation strategies to the ecology of birds. The integration of physiology and metabolism and conservation has been rarely performed but recently many authors have called for the development of physiologically explicit models to aid in the general conservation effort.

In this thesis the DEB theory is applied to a group of forty different bird species. This group was assembled as a sample of the existing diversity in terms of phylogeny, distribution and life history traits of modern birds. By looking into the diversity of DEB parameters, functions and implied properties according to different ecological factors I aimed at finding the patterns that may help to understand the fundamental trade-offs that have been described in birds. The properties and rules that characterize DEB theory could correspond to the proximate mechanisms that mediate the effect of external pressures on the evolution of birds. The characterization of primary and secondary patterns should also help to explain the trade-offs and correlations that have been previously observed between different life history traits of birds.

1.7 Outline of the dissertation

The research presented in this thesis is primarily driven by the current situation regarding the decline of biodiversity worldwide and the need to develop physiologically explicit theoretical frameworks and models that may allow for better assessments regarding the impact of global change scenarios and optimized decision-making.

The core of the research performed for the elaboration of this thesis is mostly based on the application of the Dynamic Energy Budget theory to one of the better studied groups of animals in the world and our selected case study group – the birds.

In Chapter 2 we propose the application of the DEB theory in the context of the modern study on the metabolism of birds. We explain how the database comprising the life history data of a large and representative sample of bird species was established. We also detail the main characteristics of the DEB theory and the methodology that was applied in order to estimate the core DEB parameters for the sampled species. Two different approaches to estimate the core DEB parameters are tested – one considering that the maturity maintenance rate coefficient will be equal to the somatic maintenance rate coefficient (i.e., we assume constant maturity density) and a second one considering these rate coefficients to be different (an approach that previous studies suggest only when growth data obtained at different food levels is available).

The estimated DEB parameters in this chapter allowed us to: a) to characterize the metabolism and energetics of birds as a group; b) to assess which DEB parameters are subject to higher degrees of variation, and potentially to different levels of phylogenetic inertia, in birds; c) to compare this group with other organisms that have already been characterized; and d) to identify relevant deviations from the expected relationship between intensive and design parameters with body size.

In Chapter 3 we investigate how the primary and secondary patterns determined by DEB parameters and properties are associated with a variety of ecological factors that characterize the life history of modern bird species. We start by explaining how rarely the metabolic processes have been integrated in the study of the life history evolution of birds and refer to the DEB parameters' values that have been estimated in the previous chapter for a sample of forty representative bird species.

In this chapter we characterize the species according to several ecological factors and categories. Based on observations obtained from the literature, a set of hypotheses is designed describing expectations on how DEB parameters' values could be related to these factors. The hypotheses are tested by applying the adequate statistical tests and analysing the primary and secondary patterns defined by the estimated primary and compound DEB parameters.

Considering the physical meaning of each parameter and expected relationship with body size we look for any deviation with relevant evolutionary meaning. We also apply a multiple regression analysis in order to assess which ecological factors are significantly associated with how the estimated values are distributed.

The results presented in this chapter allowed us to conclude that the distribution of values observed for many primary and compound DEB parameters is significantly explained by body size but also that factors such as the hatchling development type (within the altricial-to-precocial spectrum) and the ability to fly and migrate are particularly relevant for this purpose. We concluded that the co-evolution of the reserve mobilisation rate, somatic maintenance costs, von Bertalanffy growth rate and dry mass-specific respiration values, as suggested by our results, is consistent with the waste-to-hurry hypothesis. We also provide a broad interpretation on how the evolution of birds towards smaller body sizes and altricial strategies may have co-evolved with the emergence of flight and the exploration of new ecological niches. Finally we demonstrate how apparent trade-offs between different life history traits emerge from metabolic constraints which the DEB theory allows us to estimate and model.

In Chapter 4 we demonstrate how DEB theory may be usefully applied to model the life history of an endangered bird species in a thermodynamically explicit way. We address the case study of the Wandering Albatross (*Diomedea exulans*) – a seabird that exhibits a life cycle with some extreme characteristics and a growing pattern that besides the expected gain in body mass also includes a period of body mass decrease before fledging occurs. Previously, several hypotheses have been proposed to explain this pattern. We hypothesized that chicks and adults have similar metabolic traits regulating assimilation, growth and maturation but different locomotion costs (and therefore somatic maintenance costs). A decline in food availability before would cause the loss of body mass before fledging and the lifestyle of the adult would maintain that lower average body mass due to those higher locomotion costs.

To test this set of hypotheses we apply the DEB standard model, using a small set of life-history traits and growth curves. Our results confirmed the hypotheses and we successfully estimated the pattern of decline in food availability that explains mass recession, the daily energy intake of chicks and adults and the diet composition. Other useful metabolic estimates for the species were also estimated, such as the Field Metabolic Rate (FMR). Finally, we present conclusions regarding the application of DEB theory on a broader scale.

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2 Linking metabolism to the life history of birds through the Dynamic Energy Budget (DEB) Theory I: Estimating the parameters

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Abstract

Techniques used for the study and modelling of energy in birds can be of an experimental or theoretical nature. Thermodynamic modelling has been used when limited or no information is available. Allometry and Static Energy Budgets have been popular but have many limitations. The Dynamic Energy Budget (DEB) theory is a metabolic theory that complies with the laws of thermodynamics, unifying traits that are common to all organisms and linking different levels of biological organisation. With DEB theory, the von Bertalanffy growth curve describes the growth of organisms, at constant food levels. We applied the DEB theory on a sample of 40 species of birds representing the physiological, ecological and biogeographical diversity that currently exists in the group. The parameterization procedure was undertaken using the covariation method, providing estimates for the core DEB parameters. Single-point data and growth curves were used as input data. The von Bertalanffy growth pattern provided a good adjustment for most species. Accurate estimates for most traits were obtained using the estimated DEB parameters' values, except for the incubation period and sexual maturity, which are sometimes underestimated due to possible metabolic acceleration or inaccurate puberty related data. The allocation of energy to somatic growth and maintenance exhibited the lowest degree of variation, suggesting that it may have been subject to a high degree of phylogenetic inertia throughout the evolution of birds. Birds seem to be characterized by parameter sets that prioritize the development of soma and high growth rates, supporting the hypothesis of the waste-to-hurry strategy. The distribution of estimated primary and compound DEB parameters expected to scale with body size was consistent with that strategy. Some DEB parameters and functions not expected to scale with body size exhibited patterns suggesting otherwise. The specific allocation to reproduction per maximum structural volume decreased with increasing ultimate structural length, revealing a possible evolutionary constraint for birds. The high degree of variation observed for some parameters may explain the diversity of life history traits currently observed in birds, offering the necessary adaptive plasticity for birds to adjust to environmental change. Further studies researching the association between the distribution of DEB parameters and ecological factors may help to understand how the metabolism, ecology and behaviour of bird species may have co-evolved. By applying the DEB theory we may be able to understand how trade-offs between life history traits may have emerged from metabolic constraints and how birds may adapt to global change.

Keywords

Dynamic Energy Budget (DEB) theory; life history traits; birds; physiology; metabolism; parameter estimation

2.1 Introduction

The beginning of the modern study of metabolism and energetics in animal species has been attributed to the work of Da Vinci, Lavoisier and Laplace (Blaxter, 1989; Fort et al., 2011), several centuries ago. The development of thermodynamics as a scientific field in the 18th and 19th centuries (Gibbs, 1876; Joule, 1884; von Helmholtz, 1882) led to the study of biological thermodynamics in the 20th century (Krebs and Kornberg, 1957; Schmidt-Nielsen, 1998, 1972) and the continuous advancement of technology and miniaturisation allowed for the measurement of an increasing diversity of traits on a larger number of species (Fort et al., 2011; Kearney, 2012; Ropert-Coudert and Wilson, 2005). However, the exchange of energy between organisms and the surrounding environment, in order to build and maintain their soma and reproduction, have been studied in a very small number of animal species considering the currently known total. For instance, within a universe of about 10,500 currently known bird species, the resting metabolic rate (RMR) has only been obtained for some hundreds of species (Bennett and Harvey, 1987; Blaxter, 1989; Glazier, 2008).

Studying the energetics of birds is useful for many reasons. On a general level, it allows for a better understanding of how the energy balance is maintained throughout the life cycle of individuals and how much this balance is determined by processes such as growth, maturation, feeding and reproduction. Through the standard use of energetic units (e.g., Joules, J) comparisons across the organizational (Ernest and Brown, 2001; Harte, 2011), spatial (Davies et al., 2007; Root, 1988) and temporal scales (Brown and Adams, 1984; McWilliams et al., 2004) become possible.

On other more specific levels, several reasons can be identified. On a very practical level, these studies may contribute to fill in the gaps of knowledge regarding a large number of poorly documented species. For instance, the models used in population dynamics require data on life history traits that are lacking even for the most studied animal groups, such as the birds. In this regard, reliable data estimates are required in order to fill in the gaps and model the effects of global change for instance, in an optimized amount of time.

Within the scope of conservation physiology (Cooke et al., 2013), detailed knowledge of avian metabolism may facilitate the establishment of indices of physiological stress, allowing for better estimates on species persistence under different scenarios (e.g. land-use change, climate change and food-web disturbance) at all scales (Einoder, 2009; Ellis et al., 2012; Fort et al., 2011; Seebacher and Franklin, 2012). The need to develop mechanistic, individual-based models that may reliably simulate processes such as feeding, reproduction and death, continues to be highlighted for such purposes as linking metabolism to ecological patterns and environmental change (Seebacher and Franklin, 2012) or developing general ecosystem models (GEM) (Harfoot et al., 2014; Purves et al., 2013).

Several approaches and techniques have been used to study the metabolism of birds (Fort et al., 2011). Some of these approaches rely mostly on experimental procedures while others are fundamentally theoretical. The most common theoretical approach is probably the use of allometry. These studies have been focused on a variety of bird species, usually involving the scaling of body weight with other traits (Lislevand et al., 2007) including the Basal Metabolic Rate (BMR) (Brody and Proctor, 1932; Glazier, 2008; Hulbert and Else, 2004; Lindström and Kvist, 1995; Scott et al., 1996; White, 2011). For this purpose allometry studies usually need previous measurements of energy requirements or metabolic rates and body weight values for a number of species. The history, advantages and constraints of allometry have been frequently

reviewed in literature (White, 2011). Among the diverse number of known constraints to the use of allometric scaling relationships of an exclusively mathematical nature is the fact that these assume similarities between species based mostly on body mass, ignoring dimensional differences and the consequences that arise from these, and therefore are highly sensitive to the inclusion or exclusion of particular groups of organisms (Lynch and Fagan, 2009).

Theoretical studies relying on observed life history traits and phylogenetic trees led to some relevant insights regarding the diversity of these traits in birds. Sibly *et al.* (2012) observed strong phylogenetic signals leading to conservative trends of avian lifestyles (i.e., with similar life-history traits) within Order-level clades of birds, which may have evolved independently in different clades and Pienaar *et al.* (2013) suggested that the evolution of body and egg mass as well as of the incubation, fledging and independence periods was affected by strong phylogenetic inertia.

The use of theoretical modelling based on simple mechanistic rules to describe how species take up and use energy and mass is also becoming more common. Models that can be applied to a wide range of species have been developed, enabling estimations to be made on the state of pools and flows of energy and mass in populations, communities and ecosystems. These models may ultimately lead to the establishment of theories in ecology if currently recognized inconsistencies are addressed (van der Meer, 2006). Within this approach, thermodynamic modelling has been used when very limited or no information is available besides some morphological properties of the species. This approach uses the first principles of thermodynamics to perform theoretical calculations upon the energy requirements of species, considering a given shape, mass, and other life history traits (Fort et al., 2011, 2009). Static Energy Budgets (SEB) have been particularly popular. These studies try to capture a snapshot of the energy fluxes for an individual in a given state, frequently compiling the measurements of the energetic costs of specific activities per unit of time and then using detailed time budgets (stipulating the duration of each activity) to programme time-energy budgets and estimate the energy requirements of the species (Goldstein, 1988; Grémillet et al., 2005, 1995; Harding et al., 2009; Jürgens and Prothero, 1991; MacMillen and Carpenter, 1977). However, SEB models do not quantify the overhead costs of growth and assimilation and do not account for maturation and reproduction costs besides maintenance which is usually accounted indirectly through respiration (the uptake of dioxygen or the production of carbon dioxide and/or heat) (Kooijman, 2012). Alternatively, Dynamic Energy Budgets (DEB) follow how energy fluxes change during the life cycle of organisms (Kooijman, 2010a, 2000, 1993, 1986; Kooijman et al., 2008; Sousa et al., 2010, 2008).

The DEB theory is a metabolic theory that complies with the laws of thermodynamics, unifying traits that are common to all organisms and linking different levels of biological organisation (cells, organisms and populations) (Kooijman, 2010a; Kooijman et al., 2008). The theory uses simple quantitative and mechanistic rules that describe the uptake and use of energy and nutrients (substrates, food, light), the organisation of metabolism and the consequences for physiological organisation throughout the life cycle of organisms (Sousa et al., 2010, 2008).

Using the DEB theory, the difference between species can be reduced to differences in a single set of parameter values. Some of these parameters represent metabolic processes that are not easily measured but may correspond to the proximate mechanisms that mediate the effect of environmental selective pressures on life history traits as well as to the physiological constraints that determine the way organisms respond to change at the individual or evolutionary scales. Particularly relevant are those parameters defining priority rules in the allocation of energy to different metabolic processes.

The application of DEB theory has allowed for very detailed work in a wide range of species, covering almost all larger animal phyla and all chordate classes (Kooijman, 2013; van der Meer et al., 2014), progressively being compiled in the "Add_my_pet" library (Kooijman, 2014a). Some insights have been obtained considering this wide range of species (Kooijman, 2014b, 2013) and some studies focused on groups of species in particular, such as insects (Maino and Kearney, 2014) or marine organisms in general (Sarà et al., 2014).

The standard DEB model describes the ontogeny of an organism through the dynamics of three state variables – structure ($V = L^3$), reserve (E) and maturity (E_H) – using a set of 'primary' and 'compound' parameters. Primary parameters are connected to a single underlying process and compound parameters are simple functions of parameters, typically depending on several underlying processes.

DEB parameters can also be classified as 'core' or 'auxiliary'. Core parameters are linked to underlying assumptions of DEB theory and relate directly to processes that control the state variable dynamics, which are of an abstract nature. Auxiliary parameters link these abstract variables to quantities that can be measured directly (e.g., length, weight, respiration, etc).

Finally, DEB parameters can also be classified as 'intensive' or 'design' according to their physical meaning and relationship with body size. Intensive parameters are independent of body size. Design parameters co-variate with structural body length. The appropriate ratios of design parameters can also be intensive.

In DEB theory the use of scaling relationships includes body size as a result of underlying processes and not as an independent variable with which eco-physiological properties are regressed empirically (as in allometric relationships). Allometry is not used in DEB theory but physiological quantities (e.g., body weight) and processes (e.g., respiration) are functions of parameters. Inter-species comparisons are performed using the 'zoom factor' – the ratio between each species maximum structural body length (L_m) and that one of a reference species (which may generally be equal to 1 cm). The maximum structural body length is a compound parameter in itself, calculated from other parameters. Several primary and secondary scaling relationships rely on the way DEB primary and compound parameters relate to structural length and therefore theoretical expectations emerge whenever we compare species with differences in length.

We hypothesized that by applying the DEB theory to such a life history diverse group such as the modern birds (Neornithes), we would find that different DEB parameters would exhibit different degrees of variation, potentially representing different levels of phylogenetic inertia or phenotypic plasticity. Comparing the distribution of the estimated values for the DEB parameters of bird species with those previously obtained for other organisms could also provide valuable insights regarding the position of modern birds in the scope of the existing biodiversity.

We also hypothesized that by analysing the distribution of estimated DEB parameters' values for birds, as functions of maximum structural body length would allow us to observe any insightful deviations from the expected relationship with body size.

Taking into account the diversity of life histories currently found in birds we established a database with 40 (forty) species, integrating that diversity as much as possible, including the full range of body sizes. We then proceeded by applying two different approaches to estimate the core DEB parameters' values, depending on two different assumptions regarding maturity density. For this purpose we applied the covariation method (Lika et al., 2011a, 2011b). The

resulting parameter sets were subsequently compared and the approach offering a better adjustment between the estimated data and real data was selected for further analysis.

The values estimated for the DEB primary parameters as well as for the relevant DEB compound parameters allowed us: a) to characterize the metabolism and energetics of birds as a group; b) to assess which DEB parameters are subject to higher degrees of variation, and potentially to different levels of phylogenetic inertia, in birds; c) to compare this group with other organisms that have already been characterized; and d) to identify relevant deviations from the expected relationship between intensive and design parameters with body size.

2.2 Methodology

2.2.1 Data used

In order to address the current diversity found in birds (Table 2.1), we selected a group of species that would simultaneously cover the phylogenetic spectrum, at the taxonomic level of the Order, and the diversity of zoogeographic realms (Table 2.2). Taxonomically, we considered the classification system adopted in the World Bird List of the International Ornithologists' Union (Gill and Donsker, 2012). One species from each of the forty Orders of modern birds was selected (35 species from the Superorder Neognathae and 5 from the Palaeognathae) from breeding ranges covering all the main continents, most oceans and all the zoogeographic realms identified by Holt et al. (2012). The main constraint was data availability but we were still able to include diversity regarding a variety of life history traits (Table 2.3). Species with available growth curves were preferred and all the data had to result from measurements taken from specimens developing in *ad libitum* food availability conditions (preferably in captivity). It was not possible to include growth curves for two of the Orders, namely Leptosomiformes and Mesitornithiformes, as there were none available for the single species included in the first (the Cuckoo Roller) or any of the three species of mesites (Brown, White-breasted and Subdesert). Most of the data was collected from the literature but some values were obtained by directly consulting experts on the focused group or species.

Some life history traits were indispensable in the sense that some value had be included in order for the DEB parameters to be estimated. That is the case with the average temperatures observed in the egg throughout the incubation temperature (T_{ah}), the average adult body temperature (T_{am}) and the total body water (TBW) (which is useful to estimate specific densities). However, for some species no information was available regarding these life history traits and values measured in other phylogenetically close species were used. If no values were available from species of the same Order, values from species of other phylogenetically close Orders were considered. The phylogenetic criterion used followed the results obtained by Hackett *et al.* (2008).

Other traits such as diet, size or incubation period were also used as criteria to help select the species or group from which values were adopted (Table 2.4). No information was available regarding the incubation period (a_h) or the average age of fledglings (a_x) for the White-breasted Mesite. However, at least regarding the incubation, data was available from the Subdesert Mesite (*Monias benschi*) and this value was adopted. Data on sexual maturity, the onset of puberty or the age when the first reproductive event was observed (a_p) were also missing for some of the species. Considering that for most species there is no clear knowledge on the exact moment when sexual maturity is reached (which could correspond to months before the beginning of the first breeding season) and the first reproductive event is used as an estimate (starting with one year after hatching), there is the possibility that for these species the data is actually overestimating the development of maturity. Taking this uncertainty into consideration, observations registered for species for which this information was available were adopted following the criteria described earlier.

Finally, data on average hatchling body weight (W_w^h) was missing for three species (the Cuckoo Roller, the White-breasted Mesite and the Eared Quetzal) and values were also adopted from other species according to the same criteria (Table 2.4). The average body length (L_w^p) and body (wet) weight (W_w^p) when sexual maturity has been reached were considered to be equal to the values observed in the adult, considering that for most species the adult body size has been

reached before the first reproductive event. Nevertheless, in the cases of the species for which more detailed information was available regarding the onset of sexual maturity and the observations corresponded to an age when adult body size probably hadn't yet been reached (the Red Junglefowl, the Greater Rhea and the Red-winged Tinamou) these traits were not considered for the parameterization.

Table 2.1 – Stylized facts on birds regarding relevant physiological life history traits that are also used to estimate the core parameters of DEB theory. Each trait is complemented with one or more contextualizing comments, examples of species that display opposite extreme values for that trait and their respective bibliographical sources.

Trait	Comments	Lowest value	Highest value	Sources
Egg temperature	Embryo heat generation is limited; Egg heat dissipation from is limited; Egg temperature deviate from ambient temperature by -0.5 °C to 3 °C; Most bird embryos must develop within narrow temperature limits;	29.1 °C (*Apteryx haastii*; Great Spotted Kiwi; Apterygiformes)	42.5 °C (*Streptopelia risoria*; African Collared Dove; Columbiformes)	(Deeming and Ferguson, 1991a)
Body temperature	Avian thermoregulatory processes serve to maintain the temperature of interior tissues and organs within narrow limits; Normothermic values for most birds are higher than for mammals; Core temperatures of large flightless birds and some aquatic species fall within the mammalian range; Some insectivorous birds enter torpor (35 °C to 37.5 °C); Body temperature varies over the course of the day;	37.4 °C (*Apteryx owenii*; Little Spotted Kiwi; Apterygiformes)	42.4 °C (*Melanerpes formicivorus*; Acorn Woodpecker; Piciformes)	(Dawson and Whittow, 1999; McNab, 1996)
Total body water (TBW)	TBW in adult birds averages approximately 60% of body weight regardless of size or habitat; TBW may decrease with age; Juveniles may have higher values (80%) that decrease until fledging, possibly due to the fact that progenitors are not able to provide water to nestlings; Lower values may result from higher proportion of fat content, feathers or bone tissue, in body weight;	38.6 % (*Piranga rubra*; Summer Tanager; Passeriformes)	83.6 % (*Larus glaucescens*; Glaucous-winged Gull; Charadriiformes)	(Mahoney and Jehl Jr., 1984; Newton, 2008; Schreiber and Burger, 2002)
Incubation	Incubation is reasonably continuous; Incubation period is fixed by	10 days (*Cardellina pusilla*; Wilson's Warbler;	90 days (*Apteryx mantelli*; North Island Brown	(Deeming and Ferguson, 1991a; Schreiber and

	both genetic mechanisms and the uniform incubation conditions of temperature and humidity but seems to be more labile in seabirds;	Passeriformes)	Kiwi; Apterygiformes)	Burger, 2002)
Fledging	Characteristic of altricial birds; Feathers and wing muscles are sufficiently developed for flight; feeding autonomy;	0 days (precocial birds)	300 days (*Diomedea exulans*)	(Tickell, 1968)
Sexual Maturity	Gonad development complete; First occurrence of reproductive behaviour;	52 days (male of *Coturnix japonica*; Japanese Quail; Galliformes)	10 years (female of *Strigops habroptila*; Kakapo; Psittaciformes)	(Tacutu et al., 2013)
Maximum life span	Larger individuals have longer lives and lower per-gram resting and daily energy expenditures;	3 years (wild) (*Cardellina rubrifrons*; Red-faced Warbler; Passeriformes); 4 years (captive) (*Loxia leucoptera*; Two-barred Crossbill; Passeriformes)	80 years (*Apteryx rowi; Okarito Kiwi*; Apterygiformes)	(Furness and Speakman, 2008; NZDOC, 2013; Tacutu et al., 2013)
Body weight (hatchling)	The reserve density at birth tends to covary with that of the mother at egg production;	0.29 g (*Selasphorus sasin*; Allen's Hummingbird; Apodiformes)	816 g (*Struthio camelus*; Common Ostrich; Struthioniformes)	(Tacutu et al., 2013; Zoccarato et al., 2004)
Body weight (adult), Body length (adult)	The relationship between weight, reserves and structural volume is not exact and depends on species specific details; Energy reserves contribute to weight but are sensitive to feeding conditions; Weights usually much more scattered, in comparison to length measurements;	1.6 g, 5.5 cm (*Mellisuga helenae*; Bee Hummingbird; Apodiformes);	160 kg, 2.75 m (*Struthio molybdophanes*; Somali Ostrich; Struthioniformes)	(del Hoyo et al., 1999; Snow and Perrins, 1998; Softpedia, 2008)
Broods per year	The moment of reproduction is usually synchronised with seasonal cycles such that food availability matches the demand of the offspring;	1 (many species)	6 (Coliidae; Coliiformes)	(del Hoyo et al., 2001a)
Clutch size	Clutch size corresponds to the ratio of the reproduction buffer content to the energy costs of one chick and usually depends on food availability during the months prior to egg laying, typically decreasing if breeding is postponed in the season.	1 (many species)	up to over 30 eggs (*Leipoa ocellata*; Malleefowl; Galliformes)	(Lislevand et al., 2007)

Table 2.2 – Collection of species selected for parameterization. The taxonomy and breeding range were obtained from the classification system adopted in the World Bird List of the International Ornithologists' Union (Gill and Donsker, 2012). Breeding range abbreviations are: Africa (AF) (whole continent); Antarctica (AN); Australasia (AU) (Indonesian islands east of Wallace's Line, New Guinea and its islands, Australia, New Zealand and its subantarctic islands, the Solomons, New Caledonia and Vanuatu); Eurasia (EU) (Europe, Asia from the Middle East through central Asia north of the Himalayas, Siberia and northern China to Japan); Latin America (LA) (Middle & South America); Indian Ocean (IO); Middle America (MA) (Mexico through Panama); North America (NA) (includes the Caribbean South America (SA); Oriental Region (OR) (South Asia from Pakistan to Taiwan, plus southeast Asia, the Philippines and Greater Sundas); Pacific Ocean (PO); Southern Ocean (SO); Tropical Ocean (TrO). The Zoogeographic realms where each species is resident and/or breeding were obtained from Holt et al. (2012) and the abbreviations are: Afrotropical (AFT); Australian (AUS); Madagascan (MAD); Nearctic (NEA); Neotropical (NEO); Oceanian (OCN); Oriental (ORI); Palearctic (PAL); Panamanian (PAN); Saharo-Arabian (SAH); Sino-Japanese (SIN).

Superorder	Order	Species	Common name	Breeding range	Zoogeographic realm (breeding)
Neognathae	Accipitriformes	*Aquila chrysaetos*	Golden Eagle	NA, MA, EU	AFT, NEA, ORI, PAL, SAH, SIN
Neognathae	Anseriformes	*Anas platyrhynchos*	Mallard	NA, EU	NEA, PAL, PAN, SAH, SIN
Neognathae	Apodiformes	*Apus apus*	Common Swift	EU	PAL, SAH, SIN
Neognathae	Bucerotiformes	*Bucorvus leadbeateri*	Southern Ground Hornbill	AF	AFT
Neognathae	Caprimulgiformes	*Podargus strigoides*	Tawny Frogmouth	AU	AUS
Neognathae	Cariamiformes	*Cariama cristata*	Red-legged Seriema	SA	NEO
Neognathae	Charadriiformes	*Larus argentatus*	European Herring Gull	EU	NEA, PAL, SAH
Neognathae	Ciconiiformes	*Ciconia ciconia*	White Stork	EU	PAL, SAH
Neognathae	Coliiformes	*Urocolius macrourus*	Blue-naped Mousebird	AF	AFT
Neognathae	Columbiformes	*Columba livia*	Rock Dove	Worldwide	AFT, AUS, NEA, OCN, ORI, PAL, PAN, SAH, SIN
Neognathae	Coraciiformes	*Todiramphus cinnamominus*	Micronesian Kingfisher	PO	OCN
Neognathae	Cuculiformes	*Cuculus canorus*	Common Cuckoo	EU	ORI, PAL, SAH, SIN
Neognathae	Eurypygiformes	*Rhynochetos jubatus*	Kagu	AU	OCN
Neognathae	Falconiformes	*Falco naumanni*	Lesser Kestrel	EU	PAL, SAH, SIN
Neognathae	Galliformes	*Gallus gallus*	Red Junglefowl	OR	AUS, OCN, ORI, SIN
Neognathae	Gaviiformes	*Gavia immer*	Great Northern Loon	NA, EU	NEA, PAL
Neognathae	Gruiformes	*Gallinula chloropus*	Common Moorhen	EU, AF, IO, OR, PO	AFT, MAD, NEA, NEO, ORI, PAN, SAH, SIN
Neognathae	Leptosomiformes	*Leptosomus discolor*	Cuckoo Roller	AF	MAD
Neognathae	Mesitornithiformes	*Mesitornis variegatus*	White-breasted Mesite	AF	MAD
Neognathae	Musophagiformes	*Tauraco erythrolophus*	Red-crested Turaco	AF	AFT
Neognathae	Opisthocoformes	*Opisthocomus hoazin*	Hoatzin	SA	NEO
Neognathae	Otidiformes	*Ardeotis kori*	Kori Bustard	AF	AFT
Neognathae	Passeriformes	*Parus major*	Great Tit	EU	ORI, PAL, SAH, SIN
Neognathae	Pelecaniformes	*Pelecanus onocrotalus*	Great White Pelican	EU	AFT, ORI, PAL, SAH
Neognathae	Phaethontiformes	*Phaethon rubricauda*	Red-tailed Tropicbird	TrO	AFT, AUS, MAD, OCN, ORI, SIN
Neognathae	Phoenicopteriformes	*Phoeniconaias minor*	Lesser Flamingo	AF, OR	AFT, ORI
Neognathae	Piciformes	*Ramphastos toco*	Toco Toucan	SA	NEO
Neognathae	Podicipediformes	*Podilymbus podiceps*	Pied-billed Grebe	NA, LA	NEA, NEO, PAN
Neognathae	Procellariiformes	*Diomedea exulans*	Wandering Albatross	SO	AFT, AUS, NEO
Neognathae	Psittaciformes	*Forpus passerinus*	Green-rumped Parrotlet	SA	NEO, PAN
Neognathae	Pteroclidiformes	*Pterocles alchata*	Pin-tailed Sandgrouse	EU	PAL, SAH
Neognathae	Sphenisciformes	*Pygoscelis adeliae*	Adelie Penguin	SO, AN	NEO, AUS
Neognathae	Strigiformes	*Tyto alba*	Western Barn Owl	NA, SA, AF, EU, OR	AFT, AUS, MAD, NEA, NEO, OCN, ORI, PAL, PAN, SAH
Neognathae	Suliformes	*Phalacrocorax auritus*	Double-crested Cormorant	NA, MA	NEA, PAN
Neognathae	Trogoniformes	*Euptilotis neoxenus*	Eared Quetzal	MA	NEA
Palaeognathae	Apterygiformes	*Apteryx mantelli*	North Island Brown Kiwi	AU	AUS
Palaeognathae	Casuariiformes	*Dromaius novaehollandiae*	Emu	AU	AUS
Palaeognathae	Rheiformes	*Rhea americana*	Greater Rhea	SA	NEO
Palaeognathae	Struthioniformes	*Struthio camelus*	Common Ostrich	AF	AFT
Palaeognathae	Tinamiformes	*Rhynchotus rufescens*	Red-winged Tinamou	SA	NEO

Table 2.3 – Selected life history traits for each selected species: Tah – average incubation temperature (K); Tam – average adult body temperature (K); ah – incubation period (d); a_x – age at fledging (d); a_p – age at puberty (d); a_m –maximum life span (d); L_w – ultimate body length (from head to tail) (cm); W_w^h – hatchling wet weight (g); W_w^∞ – adult wet weight (g); $\dot{R}_\infty$ – maximum reproduction rate (# d^{-1}); W_w^∞ / W_d^∞– ratio between wet weight and dry weight (-); d_V^d – specific density of dry structural mass (g cm^{-3}). Values in italic were adapted from data observed in other related species and according to criteria detailed in the text.

Species	T_{ah} (K)	T_{am} (K)	a_h (d)	a_x (d)	a_p (d)	a_m (d)	L_w (cm)	W_w^h (g)	W_w^∞ (g)	$\dot{R}_\infty$ (# d^{-1})	W_w^∞ / W_d^∞ (-)	d_V^d (g cm^{-3})	Sources
Aquila chrysaetos	*309.7*	311.5	44.0	67.5	1.46×10^3	1.75×10^4	81.5	105.0	4.23×10^3	5.48×10^{-3}	2.4	0.42	2, 3, 34, 37, 58, 61, 144, 168, 169, 172
Anas platyrhynchos	309.7	314.2	27.5	55.0	210.0	1.06×10^4	57.5	32.4	1.06×10^3	3.01×10^{-2}	3.0	0.33	36, 45, 81, 101, 142, 143, 163, 172
Apus apus	*307.8*	312.0	20.7	42.5	730.0	7.70×10^3	16.5	2.9	40.2	6.31×10^{-3}	2.3	0.43	26, 41, 71, 124, 138, 142, 163, 172, 188
Bucorvus leadbeateri	310.2	*313.1*	42.0	86.0	730.0	2.56×10^4	109.5	55.0	3.77×10^3	5.48×10^{-3}	2.4	0.42	4, 58, 75, 90, 95, 113, 117, 166, 172
Podargus strigoides	310.2	310.8	30.0	32.5	240.0	1.46×10^4	43.5	18.0	473.8	6.85×10^{-3}	2.3	0.43	194, 4, 17, 26, 45, 57, 93, 94, 95, 164
Cariama cristata	310.2	*312.0*	27.5	30.0	240.0	1.17×10^4	90.0	61.5	2.75×10^3	5.48×10^{-3}	2.3	0.43	78, 79, 4, 43, 45, 58, 95, 151
Larus argentatus	311.3	314.2	29.0	37.5	1.1×10^3	1.79×10^4	59.5	67.5	970.6	8.22×10^{-3}	2.8	0.36	2, 38, 103, 104, 142, 143, 163, 165, 172, 184
Ciconia ciconia	*308.5*	312.5	32.0	61.0	1.46×10^3	1.42×10^4	112.5	72.5	3.30×10^3	1.33×10^{-2}	2.6	0.38	36, 39, 115, 142, 163, 172, 179, 180
Urocolius macrourus	*308.5*	312.9	12.0	12.5	*365.0*	4.38×10^3	11.1	2.3	55.8	4.11×10^{-2}	2.6	0.38	4, 20, 33, 51, 64, 137, 140, 142, 150
Columba livia	310.9	313.6	18.0	36.0	140.0	1.28×10^4	32.5	15.2	300.00	1.64×10^{-2}	2.2	0.45	40, 45, 70, 98, 142, 163, 172
Todiramphus cinnamominus	310.8	312.6	23.0	33.0	304.8	4.75×10^3	22.0	5.8	63.2	1.10×10^{-2}	2.9	0.34	12, 26, 83, 92, 135
Cuculus canorus	309.3	*313.0*	11.7	19.0	365.0	4.71×10^3	33.0	2.6	115.0	2.52×10^{-2}	2.8	0.36	19, 40, 125, 156, 163, 172, 195
Rhynochetos jubatus	310.5	*310.8*	35.0	109.0	730.0	1.1×10^4	60.0	67.5	900.0	2.74×10^{-3}	2.3	0.43	45, 17, 22, 26, 56, 86, 94, 155
Falco naumanni	*308.3*	*312.0*	28.5	28.0	365.0	3.98×10^3	30.5	10.3	151.3	1.10×10^{-2}	2.3	0.43	32, 37, 39, 43, 45, 153, 163, 172
Gallus gallus	310.5	314.0	21.0	7.0	174.3	9.13×10^3	57.0	26.7	959.3	1.64×10^{-2}	2.6	0.38	2, 6, 30, 45, 52, 59, 91, 109, 122, 132, 142, 152, 172, 187
Gavia immer	310.5	312.0	24.5	73.5	730.0	8.80×10^3	80.0	79.6	4.04×10^3	5.48×10^{-3}	2.5	0.40	2, 36, 68, 104, 163, 172, 189
Gallinula chloropus	308.0	*312.6*	21.5	45.0	365.0	6.79×10^3	33.5	13.9	320.0	3.84×10^{-2}	3.2	0.31	37, 45, 80, 128, 142, 163, 172, 192
Leptosomus discolor	*310.8*	*312.6*	20.0	30.0	*365.0*	1.01×10^4	45.0	*3.0*	225.0	1.10×10^{-2}	2.9	0.34	26, 37, 83, 92, 172, 181
Mesitornis variegatus	*310.9*	*313.6*	*24.3*	-	*365.0*	4.82×10^3	31.0	*5.0*	107.0	5.48×10^{-3}	2.2	0.45	6, 30, 40, 45, 98, 142, 159, 172
Tauraco erythrolophus	310.2	*312.0*	24.0	31.5	240.0	9.86×10^3	48.5	16.0	267.5	5.48×10^{-3}	2.5	0.40	89, 104, 129, 157, 172, 189
Opisthocomus hoazin	*310.5*	312.0	32.0	17.5	365.0	1.1×10^4	66.0	20.9	750.0	6.85×10^{-3}	2.8	0.36	2, 4, 72, 95, 118, 125
Ardeotis kori	310.5	*313.3*	23.0	31.5	730.0	1.17×10^4	116.5	99.7	9.38×10^3	4.16×10^{-3}	2.8	0.36	2, 6, 11, 77, 125, 178
Parus major	*308.4*	314.0	13.9	19.0	365.0	5.48×10^3	14.0	1.3	18.0	4.59×10^{-2}	3.0	0.33	31, 35, 39, 114, 142, 145, 163, 172, 178, 182
Pelecanus onocrotalus	310.6	*312.0*	32.5	80.0	1.1×10^3	1.86×10^4	157.5	106.2	8.90×10^3	5.48×10^{-3}	2.5	0.40	1, 36, 39, 73, 163, 154, 123
Phaethon rubricauda	308.0	311.5	45.0	79.0	274.0	1.19×10^4	79.5	54.0	717.5	2.74×10^{-3}	2.8	0.36	6, 53, 84, 104, 142, 172
Phoeniconaias minor	310.2	*312.5*	28.0	77.5	*730.0*	1.83×10^4	85.0	85.5	1.73×10^3	2.74×10^{-3}	2.8	0.36	6, 18, 24, 29, 104, 158, 163
Ramphastos toco	310.2	311.9	17.5	47.5	1.1×10^3	9.49×10^3	61.0	16.0	665.6	8.22×10^{-3}	2.9	0.34	2, 26, 69, 113, 160, 161, 167
Podilymbus podiceps	*309.5*	*312.6*	25.0	43.5	365.0	4.98×10^3	34.5	14.9	440.0	1.64×10^{-2}	2.8	0.36	2, 25, 36, 62, 104, 108, 142, 163, 172
Diomedea exulans	*308.8*	312.6	79.5	255.0	2.2×10^3	2.19×10^4	122.5	379.0	7.86×10^3	1.37×10^{-3}	2.0	0.50	2, 7, 13, 23, 36, 99, 142, 162, 163, 177, 186

Forpus passerinus	307.5	311.8	21.0	35.0	365.0	9.13×10^3	12.0	1.9	25.0	3.84×10^{-2}	3.0	0.33	15, 67, 102, 127, 149, 172, 185, 193
Pterocles alchata	*311.3*	*314.4*	22.0	30.0	365.0	9.65×10^3	35.0	13.8	309.8	6.85×10^{-3}	2.2	0.45	5, 40, 98, 100, 106, 163, 172
Pygoscelis adeliae	308.8	311.2	35.2	28.0	1.1×10^3	5.84×10^3	69.9	81.0	5.00×10^3	5.48×10^{-3}	2.0	0.50	2, 6, 27, 42, 45, 87, 141, 142, 183
Tyto alba	307.0	312.0	33.0	52.5	365	7.78×10^3	34.0	15.0	334.46	3.29×10^{-2}	2.4	0.42	37, 39, 48, 57, 60, 85, 107, 142, 163, 172, 176
Phalacrocorax auritus	310.2	313.7	26.5	24.5	730.0	8.21×10^3	82.5	34.1	1.90×10^3	1.10×10^{-2}	2.9	0.34	2, 39, 45, 55, 134, 172
Euptilotis neoxenus	*310.8*	*312.6*	22.0	30.0	1.83×10^3	9.13×10^3	34.5	*14.5*	122.50	5.48×10^{-3}	2.9	0.34	10, 26, 74, 83, 88, 92, 126, 130, 190
Apteryx mantelli	304.0	311.2	82.5	25.0	*915.0*	1.83×10^4	79.8	239.3	2.35×10^3	1.64×10^{-2}	2.6	0.38	2, 6, 21, 28, 47, 54, 65, 76, 95, 110, 111, 112, 116, 136, 147, 148
Dromaius novaehollandiae	309.0	311.0	53.0	4.5	540.0	1.46×10^4	134.0	420.0	4.25×10^4	2.74×10^{-2}	2.6	0.38	2, 6, 46, 50, 95, 105, 120, 146, 170
Rhea americana	309.5	312.7	36.0	150.0	426.0	7.30×10^3	129.0	358.6	2.25×10^4	2.05×10^{-2}	2.6	0.38	2, 6, 9, 14, 16, 44, 45, 46, 66, 82, 97, 121, 139, 172, 173
Struthio camelus	307.6	311.6	40.5	135.0	1.1×10^3	1.83×10^4	212.5	816.0	12.03×10^4	1.64×10^{-2}	2.3	0.43	6, 36, 45, 49, 63, 95, 96, 119, 142, 146, 163, 171, 172, 196
Rhynchotus rufescens	309.0	*312.6*	20.0	*7.0*	210.0	5.48×10^3	40.8	35.5	868.75	1.10×10^{-2}	2.6	0.38	6, 8, 47, 131, 133, 172, 174, 175, 191

[1] Abraham & Evans 1999; [2] ADW 2014; [3] AEF 2014; [4] ALR 2014; [5] Aourir *et al.* 2008; [6] ARKive 2014; [7] Arnould *et al.* 1996; [8] Avibirds 2014; [9] AW 2014; [10] AZA Gruiformes TAG 2009; [11] AZA 2014; [12] Bahner *et al.* 1998; [13] Battam *et al.* 2008; [14] Bazzano *et al.* 2007; [15] BB 2012; [16] BBRZ 2014; [17] Bech & Nicol 1999; [18] Bech *et al.* 1979; [19] Birkhead *et al.* 2010; [20] Bouglouan 2014; [21] Bourdon *et al.* 2009; [22] Bregulla 1987; [23] Brown & Adams 1988; [24] Brown & King 2005; [25] Brua *et al.* 1996; [26] Bryant & Hails 1983; [27] Bucher *et al.* 1986; [28] Burbidge *et al.* 2003; [29] Burch & Gailband 2000; [30] Burton & Burton 2002; [31] Carere & van Oers 2004; [32] Catry *et al.* 2011; [33] Chapman & McFarland 1971; [34] Collopy 1986; [35] Cramp & Perrins 1993; [36] Cramp & Simmons 1977; [37] Cramp & Simmons 1980; [38] Cramp & Simmons 1983; [39] Cramp & Simmons 2004; [40] Cramp 1985; [41] Cramp 1988; [42] Culik & Wilson 1992; [43] Daan *et al.* 1989; [44] Davies 2003; [45] Dawson & Whittow 1999; [46] Dawson *et al.* 1983a; [47] Dawson *et al.* 1983b; [48] De Groot 1983; [49] Degen *et al.* 1991; [50] del Hoyo *et al.* 1992; [51] del Hoyo *et al.* 2001a; [52] del Hoyo *et al.* 2001b; [53] Diamond 1975; [54] DOCNZ 2014; [55] Dunn 1975; [56] Dunning Jr. 2008; [57] Durant *et al.* 2008; [58] Dykstra *et al.* 1997; [59] ECOINDIA 2014; [60] Edwards 1987; [61] EES 2007; [62] Ellis & Jehl 2003; [63] El-Safty 2011; [64] Finke *et al.* 1995; [65] Flower 1938; [66] Folch 1992; [67] Foster & Smith 2014; [68] Fournier *et al.* 2007; [69] Gardner 1992; [70] Gayathri *et al.* 2004; [71] Glutz von Blotzheim & Bauer 1994; [72] Godoy-Vitorino *et al.* 2008; [73] Goldstein 2002; [74] González-Rojas *et al.* 2008; [75] Gunn *et al.* 2012; [76] Hackett *et al.* 2008; [77] Hallager 2005; [78] Hallager 2007; [79] Hallager 2009; [80] Hammons *et al.* 1988; [81] Heitmeyer 1998; [82] Hodes 2010; [83] Holland & Romer 2012; [84] Howell & Bartholomew 1962; [85] Howell 1964; [86] Hunt 1997; [87] Janes 1997; [88] Johnsgard 2000; [89] Jones 2014; [90] Kemp 1995; [91] Kerje *et al.* 2003; [92] Kesler & Haig 2004; [93] Körtner & Geiser 1999; [94] Körtner *et al.* 2001; [95] Kuehler & Good 1990; [96] Kurtenkov 2009; [97] Lábaque *et al.* 2010; [98] LeFebvre 1964; [99] Lequette & Weimerskirch 1990; [100] Lloyd *et al.* 2000; [101] Lokemoen *et al.* 1990; [102] LP 2014; [103] Mahoney & Jehl Jr. 1982; [104] Mahoney & Jehl Jr. 1984; [105] Maloney & Dawson 1993; [106] Marder *et al.* 1986; [107] Massemin *et al.* 1997; [108] McAllister 1963; [109] McGill 2014; [110] McLennan & McCann 1991; [111] McLennan *et al.* 2004; [112] McNab 1996; [113] McNab 2001; [114] Mertens 1987; [115] Michard-Picamelot *et al.* 2002; [116] Miles *et al.* 1997; [117] Msimanga 2004; [118] Mullner 2004; [119] Mushi *et al.* 1998; [120] Nagai *et al.* 2011; [121] Navarro *et al.* 2005; [122] North & Bell 1990; [123] O'Connor 1979; [124] Ober & Verkade 1998; [125] Ohmart *et al.* 1970; [126] Orellana 2004; [127] Pacheco *et al.* 2010; [128] Pappas *et al.* 2007; [129] Peat 2007; [130] POB 2014a; [131] POB 2014b; [132] POP 2012a; [133] POP 2012b; [134] Powell *et al.* 1996; [135] Pratt *et al.* 1987; [136] Prinzinger & Dietz 2002; [137] Prinzinger *et al.* 1991; [138] Prinzinger *et al.* 1997; [139] Prinzinger *et al.* 2003; [140] Prinzinger 1988; [141] PTAG 2005; [142] Rahn 1991; [143] Ruch Jr. & Hughes 1975; [144] Rudeen & Powers 1978; [145] Rydzewski 1978; [146] Sales 2002; [147] Sales 2005; [148] Sales 2006; [149] Sandercock *et al.* 2000; [150] Schifter 1989; [151] Schulenberg 2014; [152] Schütz *et al.* 2002; [153] Schwartz *et al.* 1977; [154] SCZ 2011; [155] SDZ 2014; [156] Seal *et al.* 1981; [157] SeaWorld 2014a; [158] SeaWorld 2014b; [159] Seddon *et al.* 2003; [160] Sedgwick 2010; [161] Seibels 2001; [162] Shaffer *et al.* 2001; [163] Snow & Perrins 1998; [164] Snow 2008; [165] Spaans 1971; [166] Spear *et al.* 2005; [167] St. Leger *et al.* 2012; [168] Stinson *et al.* 1976; [169] Sumner 1929; [170] Swarbrick 2009; [171] Swart *et al.* 1993; [172] Tacutu *et al.* 2013; [173] TCP 2014; [174] Tholon & de Queiroz 2007; [175] Tholon & de Queiroz 2011; [176] Thouzeau 1999; [177] Tickell 1968; [178] Tieleman *et al.* 2002; [179] Tortosa & Castro 2003; [180] Tsachalidis *et al.* 2005; [181] Twearth 2014; [182] van Balen 1973; [183] Vleck & Vleck 2002; [184] Walter & Hughes 1978; [185] Waltman & Beissinger 1992; [186] Warham 1971; [187] Weiss 1958; [188] Weitnauer 1983; [189] Welch 2014; [190] Williamson 1992; [191] Withers *et al.* 1987; [192] Wood 1974; [193] WPT 2014; [194] WPZ 2012; [195] Wyllie 1981; [196] Zoccarato *et al.* 2004;

Table 2.4 – Reference species from which data was adapted in order to fill information gaps in indispensable life history traits such as the average temperatures observed in the egg throughout the incubation temperature (T_{ah}), the average adult body temperature (T_{am}) and the total body water (TBW) as well as in other traits such as the incubation period (a_h), the age at puberty (a_p), the maximum life span (a_m) and the hatchling wet weight (W_w^h) (g). The criteria used to select the reference species or group, from within the available data, are summarized between brackets.

Species	Reference species	Sources
Aquila chrysaetos	T_{ah}: *Haliaeetus leucocephalus* and *Pandion haliaetus* TBW: *Haliaeetus leucocephalus*	17, 38
Apus apus	T_{ah}: Five other species of Apodiformes TBW: *Collocalia esculenta*	9, 34
Bucorvus leadbeateri	T_{am}: *Rhyticeros plicatus* TBW: *Haliaeetus leucocephalus*, (Accipitriformes) (diet and size)	17, 20, 30,
Podargus strigoides	TBW: *Collocalia esculenta* (Apodiformes) (phylogeny) and *Tyto alba*(Strigiformes) (diet and size)	9, 16, 20,
Cariama cristata	T_{am}: *Falco tinnunculus* and *Falco sparverius* (Falconiformes) (phylogeny and diet) TBW: *Falco tinnunculus* (Falconiformes) (diet and phylogeny) and *Haliaeetus leucocephalus* (diet and size)	13, 14, 17, 20
Larus argentatus	TBW: Five other species within the genus *Larus*	35, 41
Ciconia ciconia	T_{ah}: Three other species of Ciconiiformes	34
Urocolius macrourus	T_{ah}: *Cyanistes caeruleus* (Passeriformes) (egg size and incubation period) a_p: *Colius striatus* TBW: *Aratinga cunicularis* (Psittaciformes) (phylogeny, diet and size)	6, 10, 20, 34
Todiramphus cinnamominus	TBW: *Merops viridis*	9
Cuculus canorus	T_{am}: Cuculiformes TBW: *Geococcyx californianus*	5, 31, 33
Rhynochetos jubatus	T_{am}: *Podargus strigoides* (Caprimulgiformes) (phylogeny, diet and size) TBW: *Collocalia esculenta* (Apodiformes) (phylogeny)	3, 9, 14, 20, 24
Falco naumanni	T_{ah}: *Falco peregrinus* and *Falco mexicanus* T_{am}: *Falco tinnunculus* and *Falco sparverius* TBW: *Falco tinnunculus*	13, 14, 36
Gavia immer	TBW: *Gavia arctica*	28
Gallinula chloropus	T_{am}: *Fulica atra* TBW: *Rallus longirostris*	21
Leptosomus discolor	T_{ah}, T_{am}: *Todiramphus cinnamominus* (Coraciiformes) (phylogeny, diet and incubation period) a_p, a_m: *Asio otus* (Strigiformes) (phylogeny, size and incubation period) TBW: *Merops viridis* (Coraciiformes) (phylogeny) W_w^h: *Asio otus* (Strigiformes) (phylogeny, size and incubation period)	9, 11, 20, 22, 23, 39
Mesitornis variegatus	T_{ah}, T_{am}: *Columba livia* (Columbiformes) (phylogeny) a_h: *Monias benschi* a_p, a_m: *Streptopelia turtur* (Columbiformes) (phylogeny) W_w^h: *Zenaida macroura* (Columbiformes) (phylogeny and size) TBW: *Columba livia* (Columbiformes) (phylogeny)	12, 14, 20, 26, 34, 37, 39
Tauraco erythrolophus	T_{am}: Gaviiformes (phylogeny)	20, 28, 42

	TBW: *Gavia arctica* (Gaviiformes) (phylogeny)	
Opisthocomus hoazin	T_{ah}, TBW: *Geococcyx californianus* (Cuculiformes) (phylogeny)	20, 25, 31
Ardeotis kori	T_{am}: *Chlamydotis undulata* TBW: *Geococcyx californianus* (Cuculiformes) (phylogeny and diet)	20, 31, 40
Parus major	T_{ah}: Passeriformes	34
Pelecanus onocrotalus	T_{am}: *Pelecanus erythrorhynchos* TBW: marine birds	1, 19
Phaethon rubricauda	TBW: *Podiceps nigricollis* (Podicipediformes) (phylogeny)	20, 28
Phoeniconaias minor	T_{am}: *Phoenicopterus ruber* a_p: Three other species of Phoenicopteriformes TBW: *Podiceps nigricollis* (Podicipediformes) (phylogeny)	4, 8, 20, 28
Ramphastos toco	TBW: *Merops viridis* (Coraciiformes) (phylogeny)	9, 20
Podilymbus podiceps	T_{ah}, T_{am}: *Podiceps nigricollis* a_m: Six other species of Podicipediformes TBW: *Podiceps nigricollis*	18, 28, 34, 39
Diomedea exulans	T_{ah}: *Phoebastria immutabilis* and *Phoebastria nigripes*	34
Pterocles alchata	T_{ah}: *Pterocles orientalis* T_{am}: *Pterocles senegallus* a_m: *Columba livia* and *Streptopelia decaocto* (Columbiformes) (phylogeny) TBW: *Columba livia* (Columbiformes) (phylogeny)	2, 20, 26, 29, 39
Euptilotis neoxenus	T_{ah}, T_{am}: *Todiramphus cinnamominus* (Coraciiformes) (phylogeny, diet and incubation period) TBW: *Merops viridis* (Coraciiformes) (phylogeny and diet) W_w^h: *Pharomachrus mocinno*	9, 20, 22, 23, 32
Apteryx mantelli	a_p: Apterygiformes TBW: *Dromaius novaehollandiae* (Casuariiformes) (phylogeny and habitat)	7, 15, 20
Rhea americana	TBW: *Dromaius novaehollandiae* (Casuariiformes) (phylogeny and diet)	15, 20
Rhynchotus rufescens	T_{am}: *Nothoprocta perdicaria* a_m: *Tinamus solitarius* TBW: *Dromaius novaehollandiae* (Casuariiformes) (phylogeny)	15, 20, 39, 43

[1] Abraham & Evans 1999; [2] Aourir *et al.* 2008; [3] Bech & Nicol 1999; [4] Bech *et al.* 1979; [5] Birkhead *et al.* 2010; [6] Bouglouan 2014; [7] Bourdon *et al.* 2009; [8] Brown & King 2005; [9] Bryant & Hails 1983; [10] Chapman & McFarland 1971; [11] Cramp & Simmons 1980; [12] Cramp 1985; [13] Daan *et al.* 1989; [14] Dawson & Whittow 1999; [15] Dawson *et al.* 1983; [16] Durant *et al.* 2008; [17] Dykstra *et al.* 1997; [18] Ellis & Jehl 2003; [19] Goldstein 2002; [20] Hackett *et al.* 2008; [21] Hammons *et al.* 1988; [22] Holland & Romer 2012; [23] Kesler & Haig 2004; [24] Körtner & Geiser 1999; [25] Kuehler & Good 1990; [26] LeFebvre 1964; [27] Mahoney & Jehl Jr. 1982; [28] Mahoney & Jehl Jr. 1984; [29] Marder *et al.* 1986; [30] McNab 2001; [31] Ohmart *et al.* 1970; [32] Orellana 2004; [33] Prinzinger *et al.* 1991; [34] Rahn 1991; [35] Ruch Jr. & Hughes 1975; [36] Schwartz *et al.* 1977; [37] Seddon *et al.* 2003; [38] Stinson *et al.* 1976; [39] Tacutu *et al.* 2013; [40] Tieleman *et al.* 2002; [41] Walter & Hughes 1978; [42] Welch 2014; [43] Withers *et al.* 1987;

2.2.2 Parameter estimation

In order to estimate the values for the core DEB parameters (Table 2.5) we used the software DEBtool (MATLAB version 7.3.0) (Kooijman, 2010b). For the purpose of running DEBtool's routines, two files for each species were programmed in MATLAB (The MathWorks Inc., 2012), using as input information the set of single-point data previously collected concerning all the relevant life history traits presented in Table 2.3. This set is henceforth designated as zerovariate data. Growth curves, characterized from measured wet weight values obtained in different time points after hatching, were also used as input and are designated as univariate data. Besides the zero and univariate data we also had to use as input initial parameter values to start the estimation procedure with. This procedure followed the "covariation method" (Lika et al., 2011a). With this method, parameter estimates are based on the simultaneous minimization of a weighted sum of squared deviations or of the negative log-likelihood function between the data we inserted and the estimated values, both in a single-step procedure. Similarly to what has been done in previous studies on avian development modelling (Huin and Prince, 2000; Weimerskirch et al., 2000a) we chose a weighted least squares criterion to fit the estimates to the set of zero and univariate data.

Auxiliary parameters were used to convert volume, mass, energy and physical measurements or to correct rates according to each specific average adult body temperature (Table 2.6). Details regarding each of these parameters are available in Lika et al. (2011a).

A predetermined value was assigned to some parameters. The reference temperature (T_{ref}) of 293 K and Arrhenius temperature (T_A) of 1.5×10^4 were chosen in order to maintain comparability with the parameter sets estimated for other species and available in the "Add_my_pet" library (Kooijman, 2014a). The same logic justified the choice of a value of 0.01 for the Gompertz stress coefficient (s_G). Food availability was included as a variable through the "scaled functional response" (f), a dimensionless variable based on the Michaelis-Menten function ($f = X / (K + X)$), also regarded as a Holling type II functional response, where X represents food and K represented the half-saturation coefficient or Michaelis-Menten constant. At any moment f can assume a value from 0 (absence of food) to 1 (*ad libitum* food available). In this study we considered a constant $f = 1$ for all the species and the growth rate we obtain corresponds to the von Bertalanffy type. A value of 0.8 was assigned to the digestion efficiency (κ_X) based on nitrogen-corrected energy assimilation efficiencies measured in several bird species (Adams, 1984; Battam et al., 2010; Cooper, 1978). The reproductive efficiency (κ_R) value was chosen by default to be 0.95, just it has previously been used for other species (Kooijman, 2014a). Detailed data regarding this type of efficiency is very rare. The surface-specific somatic maintenance ($\{\dot{p}_T\}$), that covers the costs of keeping a constant body temperature, was considered to be zero on the assumption that we are modelling growth within the thermal-neutral zone of all the different species. This assumption is particularly reasonable for birds considering the thermal insulation provided by the feathers. The chemical potentials considered for structure (μ_V) and reserve (μ_E) were the default values of 500 and 550 kJ mol^{-1}, respectively. The chemical indices for structure (n_V) and reserve (n_E) were considered to be identical and corresponded to 1 atom of carbon, 1.8 atoms of hydrogen, 0.5 atoms of oxygen and 0.15 atoms of nitrogen, per atom of carbon respectively. These are approximate default values for dry mass previously used in the absence of more detailed information on the chemical composition of the species (Lika et al., 2011a). The molecular weights of structure (w_V) and reserve (w_E) are obtained from these indices and are therefore also equal (23.9 g mol^{-1}).

The specific density of dry structural mass (d_V^d) (g cm^{-3}), for each species, was calculated using the ratio between the wet weight and dry weight observed (W_w^∞ / W_d^∞) (-) for each species (Table 2.3) and considering the typical specific density of wet structural mass (d_V^w) of 1 (one) g cm^{-3} ($d_V^d = d_V^w/((W_w^\infty)/(W_d^\infty))$. The specific density of reserve (d_E) was considered to be identical to this value.

Using the primary parameters (core and auxiliary), some useful compound parameters were computed at the reference temperature (T_{ref} = 293 K), namely the zoom factor ($z = L_m/ L_m^{ref} = \kappa \{\dot{p}_{Am}\}/ [\dot{p}_M]$) (-), with $L_m^{ref} = 1$ cm, the maximum structural length ($L_m = [E_G]\, \dot{v} / [\dot{p}_M]\, g$) (cm) (which in this case will be equal to the zoom factor), the energy investment ratio ($g = [E_G]\, \dot{v} / \kappa \{\dot{p}_{Am}\}$) (-), the somatic maintenance rate coefficient ($\dot{k}_M = [\dot{p}_M]/[E_G]$) (d^{-1}), the maximum reserve capacity ($[E_m] = \{\dot{p}_{Am}\} / \dot{v}$) (J cm^{-3}) and the von Bertalanffy growth rate, ($\dot{r}_B = 1 / (3 / \dot{k}_M + 3 f L_m / \dot{v})$) (d^{-1}) (Table 2.10).

We also computed two other ecologically important traits, namely the dry mass-specific respiration (-J_O / W_d) (L g^{-1} h^{-1}) and the fasting capacity ($t_s = [E_m] / [\dot{p}_M]$) (d) (the amount of time during which the organism, once deprived of food, still has enough energy stored in reserve to cover the specific somatic maintenance costs) (Table 2.10).

Among the many useful properties that are possible to obtain from specific DEB parameters (Kooijman, 2010a), we selected four additional ones, namely the maximum wet weight per ultimate structural volume (W_w^m / L_∞^3) (g cm^{-3}), the initial egg mass (i.e., the energy investment per offspring) (M_E^0) (C-mol), the specific allocation to reproduction per maximum structural volume as well ($\dot{p}_R^m$ / L_m^3 = (1 – κ) ([$\dot{p}_M$] / κ) – $\dot{p}_J^p$ / L_m^3) (J d^{-1} cm^{-3}) and the maturity maintenance at puberty per maximum structural volume ($\dot{p}_J^p$ / L_m^3 = $\dot{k}_J$ E_H^p / L_m^3) (J d^{-1} cm^{-3}), all at the reference temperature (Table 2.10). Considering that the parameterization of our sampled species was performed for *ad libitum* (f = 1) circumstances and that the presence of endothermy and of structural elements evolved to reduce energy expenses with heating are common to all these species, the maximum structural volume (L_m^3) equals the ultimate structural volume (L_∞^3).

The rates obtained at the reference temperature were also converted to the corresponding values at each specific average adult body temperature (T_{am}) (Table 2.3), using a temperature correction factor (TC) obtained with the Arrhenius temperature (T_A = 1.5 × 10^4 K) through the following equation: $TC = \exp((T_A - T_{ref}) / (T_A - T_{am}))$ (Table 2.11).

The covariation method also makes use of pseudo-data. This data includes typical values for a few DEB parameters (κ, $\dot{v}$, [$\dot{p}_M$], $\dot{k}_J$, and a growth efficiency κ_G = [M_V] μ_V / [E_G]) according to a generalized animal model (Kooijman 2010a, Table 8.1) and include the following values: κ = 0.8, $\dot{v}$ = 0.02 cm d^{-1}, [$\dot{p}_M$] = 18 J d^{-1} cm^{-3}, $\dot{k}_J$ = 0.002 d^{-1} and κ_G = 0.8. The application of weight coefficients to the input data and to the pseudo-data determines the relative influence each data point has on the estimation procedure. However, the relative contribution of these values to the estimation of DEB parameters for our sample of bird species was extremely low. Enough input data with the necessary accuracy was available for all the sampled species and therefore the weight coefficients applied to these values were several orders of magnitude higher than the default contribution of pseudo-data. The distribution patterns observed for the DEB parameters in our sample, diverging from the pseudo-data values also illustrate the low contribution from the pseudo-data. The only pseudo-data value that was relatively important for the parameterization of our species was the growth efficiency (κ_G). Generally we considered

that this efficiency value should not differ substantially among our species and in the absence of real data on this matter, it should also not diverge much from the standard value of 0.8.

By applying the covariation method we estimated the values for the relevant standard DEB model core parameters that provide the best estimates for all the life history traits considered while simultaneously allowing for a good fit to the observed wet weight growth curves.

Lika *et al.* (2011a) assigned different levels of completeness to the data sets used depending on how much information is present. The inclusion of wet body weight growth curves as functions of age at one constant (abundant) food level for most of the selected species corresponds to a level of completeness of 2 (two). For the two previously referred species for which this data was not available (the Cuckoo Roller and the White-breasted Mesite) the level of completeness considered was 1 (one).

Table 2.5 – The core parameters of the standard DEB model and their respective summarized descriptions. More details are available in Lika et al. (2011).

Parameter	Abbreviation	Summarized description
Surface-specific maximum assimilation rate (J d^{-1} cm^{-2})	$\{\dot{p}_{Am}\}$	Controls the assimilation of energy from ingested food.
Zoom factor (-)	z	Controls the maximum length via the surface-specific assimilation.
Maximum surface-area-specific searching rate (dm^3 d^{-1} cm^{-2})	$\{\dot{F}_m\}$	Controls food intake if food is not abundant and has no effect at abundant food.
Digestion efficiency (-)	κ_X	Specifies the fraction of energy in food that is fixed in reserve.
Defecation efficiency (-)	κ_X^P	Specifies the fraction of energy in food that ends up as faeces.
Energy conductance (cm d^{-1})	$\dot{v}$	Controls the reserve mobilisation.
Allocation fraction to soma (-)	κ	Controls the allocation of mobilised reserve to somatic maintenance and growth as opposed to maturity maintenance and maturation of reproduction.
Reproduction efficiency (-)	κ_R	Fraction of reserve allocated to reproduction that is fixed in the reserve of offspring.
Volume-specific somatic maintenance rate (J d^{-1} cm^{-3})	$[\dot{p}_M]$	Controls the sink of reserve linked to structural volume, mostly due to turnover of structure, behaviour and transport.
Surface-specific somatic maintenance rate (J d^{-1} cm^{-2})	$\{\dot{p}_T\}$	Controls the sink of reserve linked to structural surface area.
Maturity maintenance rate coefficient (d^{-1})	$\dot{k}_J$	Controls the sink of reserve linked to maturity.
Specific cost for structure (J cm^{-3})	$[E_G]$	Reserve energy required to synthesize a unit volume of structure.
Maturity at birth (J)	E_H^b	Controls the timing of and the size at birth, i.e., the moment assimilation is switched on.
Maturity at fledging (J)	E_H^x	Controls the timing of fledging, i.e., the moment at which self-feeding starts.
Maturity at puberty (J)	E_H^p	Controls the timing of and the size at puberty, i.e., the moment at which investment into maturation is re-directed to reproduction.
Weibull ageing acceleration (d^{-2})	$\ddot{h}_a$	Controls the mean life span in a way that hardly depends on food density (because the increased respiration is cancelled by dilution by growth).
Gompertz stress coefficient (-)	s_G	Controls the mean life span, but in ways that depend on food density.

Table 2.6 – Temperature and auxiliary parameters of the standard DEB model. These were used to correct for temperatures and to convert volume, mass, energy and physical measurements (Lika et al., 2011a).

Parameter	Abbreviation	Summarized description
Reference temperature (K)	T_{ref}	Working temperature for which parameter values are given.
Arrhenius temperature (K)	T_A	Controls the effect of temperature on rates.
Egg incubation temperature (K)	T_{ah}	Average temperature measured in the egg during the incubation period.
Adult body temperature (K)	T_{am}	Average temperature measured during the adult stage and considering the whole day cycle.
Shape coefficient (-)	δ_M	Converts physical to volumetric structural length and requires information on how the length is taken (e.g., from head to tail).
Specific densities (g cm^{-3})	d_V, d_E	Convert volume to mass for each organic compound (V indicates structure and E reserve).
Chemical potentials (J mol^{-1})	μ_V, μ_E	Convert moles to energy.
Chemical indices (# C^{-1})	n_V, n_E	Relate the frequency of chemical elements (C, H, O and N) to C.
Molecular weights (g mol^{-1})	w_V, w_E	The molecular weight of each organic compound is obtained by multiplying the chemical indices with the atomic mass of each element (C = 12 g mol^{-1}; H = 1 g mol^{-1}; O = 16 g mol^{-1}; N = 14 g mol^{-1}).

2.2.3 Two approaches: $\dot{k}_J = \dot{k}_M$ and $\dot{k}_J \neq \dot{k}_M$

Previous studies explained how the inclusion of extra information that may be available for the species being parameterized allows for the estimation of parameter values with progressively higher levels of detail (Kooijman et al., 2008; Sousa et al., 2010). When data regarding the growth is available from different specimens that were reared at different food availability contexts (food density), which are also known, then it is possible to estimate how the length at each stage transition is affected by food availability, and consequently the maturity maintenance rate coefficient ($\dot{k}_J$) may be determined independently from the somatic maintenance rate coefficient ($\dot{k}_M$). When this data is not available it is usual to assume a constant maturity density ($\dot{k}_J = \dot{k}_M$), which implies that metabolic switches occur at fixed amounts of structure (maturity thresholds are replaced by structure thresholds and maturity is avoided as a state variable).

Growth data sets at different food density levels are extremely rare and were not available for the species in our sample. However, we anticipated the possibility that assuming a constant maturity density would not adjust adequately to the development of many bird species that approach their asymptotic average adult (ultimate) size before important maturity thresholds are reached, such as fledging or sexual maturity. In order to assess which is more adequate for modelling the life cycle of birds, we chose to apply the covariation method using these two different approaches (i.e., assuming $\dot{k}_J = \dot{k}_M$ and $\dot{k}_J \neq \dot{k}_M$) and compared the resulting parameter sets, particularly the estimated values for the main core DEB parameters and their respective variation. Considering that the parametrization process allows for a measure of goodness of fit ("FIT" value) to be estimated (Lika et al., 2011a), going from 0 (zero) (no fit) to 10 (perfect fit), expressing the relative adjustment between the predictions calculated with the estimated parameter values to the values observed in nature and used as input (zero and univariate data), we also compared these parameter sets in order to discuss both approaches. After this step, the approach considered to be the most appropriate was taken into consideration and its respective results were selected for statistical analyses and discussion.

2.2.4 Statistical analysis

In order to investigate whether significant differences were present between the two approaches (assuming $\dot{k}_J = \dot{k}_M$ and $\dot{k}_J \neq \dot{k}_M$) and regarding one or more core DEB parameters, we used the nonparametric Mann-Whitney U test, after testing and rejecting the assumptions required for the Student's t-test (using the Shapiro–Wilk test to check the occurrence of normality in both samples and the Levene's test to check the occurrence of homocedasticity). The same tests were applied to other relevant data (e.g., input data such as incubation duration) for discussion purposes.

After estimating the DEB parameter sets for all the sampled species, an exploratory data analysis was performed. The mean ($\bar{x}$), standard error (SE), median ($\tilde{x}$), lower quartile (Q_1), upper quartile (Q_3) and coefficient of variation (c_v) were calculated for every parameter. These statistics allowed us to compare the distributions and the different degrees of variation exhibited by the DEB parameters of modern birds as well as to discuss their possible evolutionary significance in terms of phylogenetic inertia. DEB parameters were compared both at a reference temperature of 293 K and at each specific average adult body temperature. Comparing the parameter values at a shared reference temperature is useful to point out differences between species or groups of species while the discussion dealing with parameter values at the average adult body temperatures holds particular ecological and evolutionary

relevance considering that natural selection and selective pressures act upon the individuals at those temperatures and with those metabolic rates.

2.2.5 Comparing birds to other organisms

In order to contextualize the diversity and patterns of DEB parameters for birds within the broader diversity of extant living organisms, these values were plotted against a background composed by the values for the same DEB parameters that were previously estimated for 343 other species (from all larger animal phyla and all chordate classes) by many authors and that currently constitute the "Add_my_pet" library (Kooijman, 2014a). These plots allow us to analyse the primary patterns (involving a single primary parameter) as well as the secondary patterns (implied properties and functions involving two or more primary parameters).

Considering that some of the DEB parameters (primary and compound) are intensive (i.e., independent of body size) and others are considered to be design parameters (i.e., expected to scale with body size) (Table 2.7) all the values were plotted as functions of the ultimate structural length, L_∞ (cm). The only exception was for the case of the dry mass-specific respiration ($-J_O / W_d$, L g^{-1} h^{-1}) which was plotted as a function of the maximum dry mass, (W_d^m) (g). The DEB theory describes body size as the result of underlying processes and therefore interactions between these properties are to be expected.

In order to enrich the analysis, the expected DEB parameters' values for the generalized animal were also plotted as lines in each plot (Kooijman 2010a, Table 8.1). Any deviation from expectations (intensive parameters scaling with body size or design parameters deviating from the expected scaling relationship with body size) was noted and discussed.

Table 2.7 – The analysed primary and compound DEB parameters and their relationship with body size (physical meaning). Primary parameters are connected to a single underlying process and compound parameters are simple functions of parameters, typically depending on several underlying processes. DEB parameters which are intrinsically independent of body size are designated as being 'intensive', while those that are expected to scale body size are classified as 'design' parameters. The expected scaling with the ultimate structural body length for design parameters is also indicated. The dry mass-specific respiration ($-J_O$ / W_d, L g^{-1} h^{-1}) is expected to decrease with the maximum dry weight to the power ¼ (Maino et al., 2014).

Parameter	Abbreviation	Type	Physical meaning	Scales with
Surface-specific maximum assimilation rate (J d^{-1} cm^{-2})	$\{\dot{p}_{Am}\}$	primary	design	L_∞
Allocation fraction to soma (-)	κ	primary	intensive	-
Energy conductance (cm d^{-1})	$\dot{v}$	primary	intensive	-
Volume-specific somatic maintenance rate (J d^{-1} cm^{-3})	$[\dot{p}_M]$	primary	intensive	-
Maturity at birth (J)	E_H^b	primary	design	L_∞^3
Maturity at fledging (J)	E_H^x	primary	design	L_∞^3
Maturity at puberty (J)	E_H^p	primary	design	L_∞^3
Maturity maintenance rate coefficient (d^{-1})	$\dot{k}_J$	primary	intensive	-
Specific cost for structure (J cm^{-3})	$[E_G]$	primary	intensive	-
Weibull ageing acceleration (d^{-2})	$\ddot{h}_a$	primary	design	L_∞
Somatic maintenance rate coefficient (d^{-1})	$\dot{k}_M$	compound	intensive	-
Maximum reserve capacity (J cm^{-3})	$[E_m]$	compound	design	L_∞
von Bertalanffy growth rate (d^{-1})	$\dot{r}_B$	compound	design	L_∞^{-1}
Dry mass-specific respiration (L g^{-1} h^{-1})	$-J_O$ / W_d	compound	design	$W_d^{m-¼}$
Fasting capacity (d)	t_s	compound	design	L_∞
Maximum wet weight per ultimate structural volume (g cm^{-3})	W_w^m / L_∞^3	compound	design	L_∞
Initial egg mass (C-mol)	M_E^0	compound	design	L_∞^4
Specific allocation to reproduction per maximum structural volume (J d^{-1} cm^{-3})	$\dot{p}_R^m$ / L_m^3	compound	intensive	-
Maturity maintenance at puberty per maximum structural volume (J d^{-1} cm^{-3})	$\dot{p}_J^p$ / L_m^3	compound	intensive	-
Dry mass-specific maturity at birth (hatching) ($\mu_H^b = E_H^b$ / M_V^b) (J mol^{-1})	μ_H^b	compound	intensive	-
Dry mass-specific maturity at fledging ($\mu_H^x = E_H^x$ / M_V^x) (J mol^{-1})	μ_H^x	compound	intensive	-
Dry mass-specific maturity at puberty ($\mu_H^p = E_H^p$ / M_V^p) (J mol^{-1})	μ_H^p	compound	intensive	-
Puberty/birth altriciality index ($s^{pb}_H = E_H^p$ / E_H^b) (-)	s^{pb}_H	compound	intensive	-
Fledging/birth altriciality index ($s^{xb}_H = E_H^x$ / E_H^b) (-)	s^{xb}_H	compound	intensive	-

2.3 Results

2.3.1 Parameterization

The core DEB parameters' values were estimated through the covariation method and considering two approaches: a) with independent maintenance rate coefficients ($\dot{k}_J \neq \dot{k}_M$); and b) with constant maturity density ($\dot{k}_J = \dot{k}_M$). The estimated values were compared and significant differences were observed between the values obtained through each approach for the following core DEB parameters: κ, $\dot{k}_J$, E_H^b and E_H^x (Table 2.8). The value of κ estimated with $\dot{k}_J \neq \dot{k}_M$ is significantly higher than the alternative (U (78) = 52.00, $n_1 = n_2 = 40$, $p < 0.0001$). The value of $\dot{k}_J$ when estimated independently is significantly lower (U (78) = 0, $n_1 = n_2 = 40$, $p < 0.0001$). The values of E_H^b and E_H^x are also significantly lower when both maintenance rate coefficients are estimated independently (U (78) = 111, $n_1 = n_2 = 40$, $p < 0.0001$; and U (76) = 294, $n_1 = n_2 = 39$, $p < 0.0001$, respectively).

The von Bertalanffy growth curves provided good fits to the observed growth curves for most species but for some species the adjustment was not so precise (Appendix I).

A larger dispersion of κ values (higher standard error with lower and upper quartiles further apart) resulted when maintenance rate coefficients were set equal. The same observations can be made regarding the other parameters for which significantly differences were found. These results express some of the challenges observed during the parameterization process when maturity density was considered to be constant. For some species of birds this assumption does not hold easily considering that the maturity stage transitions do not seem to occur at observable specific fixed lengths. For instance, the Wandering Albatrosses reaches the adult size in less than a year but sexual maturity appears to be reached much later as these birds reproduce for the first time on average at the age of six years old. The Greater Rhea and the Red-winged Tinamou seem to reach sexual maturity before approaching the asymptotic average adult body size. In other species the differences may not be as clear but they are nevertheless present. This observation agrees with the experimental observations of Starck (1998) that led him to conclude that somatic growth and maturity follow independent ontogenetic trajectories after comparing the rates of cellular proliferation through the embryonic stage with the development of functional maturity.

When the somatic growth is quicker than maturity development, equalling both maintenance rate coefficients and maintaining a balance between the relative contributions of each kind of data to the covariation method, may force a delay in somatic growth that decreases the adjustment to the growth data considered, resulting in a lower κ value. Allowing both coefficients to change independently enables a better adjustment between the estimates and the observed data of both kinds – somatic and maturity related. This is also why regarding the goodness of fit (the "FIT" value) a significant difference was also observed. The goodness of fit was significantly higher using $\dot{k}_J \neq \dot{k}_M$ ($\bar{x}$ = 9.4±0.4; $\tilde{x}$ = 9.4) compared to $\dot{k}_J = \dot{k}_M$ ($\bar{x}$ = 9.2±0.4; $\tilde{x}$ = 9.1) (U (78) = 550, $n_1 = n_2 = 40$, $p = 0.016$).

Taking all of these facts into consideration we selected the first approach whereby both maintenance rate coefficients are independently estimated and maturity density is not necessarily constant throughout the development of birds. The DEB parameters' values estimated through this approach were the ones that we proceeded to analyse.

Table 2.8 – Descriptive statistics of selected core DEB parameters' values previously estimated through the covariation method using two different approaches: k̇J ≠ k̇M and k̇J = k̇M. The analysed parameter values are at the reference temperature (Tref = 293 K). The parameter abbreviations and their corresponding names are the following: {ṗAm} – maximum specific assimilation rate (J d-1 cm-2); κ – allocation fraction to soma (-); v̇ – energy conductance (cm d-1); [ṗM] – volume-specific somatic maintenance rate (J d-1 cm-3); EbH – maturity at birth (hatching) (J); ExH – maturity at fledging (J); EpH – maturity at puberty (J); k̇J – maturity maintenance rate coefficient (d-1); [EG] – specific cost for structure (J cm-3); ẗa – Weibull ageing acceleration (d-2); FIT – goodness of fit between estimated and observed trait values. Statistical abbreviations are as follow: $\bar{x}$ – mean; SE – standard error; $\tilde{x}$ – median; Q1 – lower quartile; Q3 – upper quartile; cv – coefficient of variation. Statistical significance is indicated as follows: * p < 0.05; **** p < 0.0001.

Approach		$\{\dot{p}_{Am}\}$ (J d^{-1} cm^{-2})	κ (-)	$\dot{v}$ (cm d^{-1})	$[\dot{p}_M]$ (J d^{-1} cm^{-3})	E_H^b (J)	E_H^x (J)	E_H^p (J)	$\dot{k}_J$ (d^{-1})	$[E_G]$ (J cm^{-3})	$\ddot{h}_a$ (d^{-2})	FIT
$\dot{k}_J \neq \dot{k}_M$	$\bar{x}$	5.34 × 10^{2}	0.988	0.14	65.30	1.83 × 10^{4}	2.97 × 10^{5}	1.07 × 10^{7}	2.29 × 10^{-5}	1.01 × 10^{4}	5.43 × 10^{-15}	9.42
	SE	50.88	5.19 × 10^{-3}	1.55 × 10^{-2}	6.22	1.44 × 10^{4}	1.13 × 10^{5}	4.19 × 10^{6}	1.46 × 10^{-5}	1.93 × 10^{2}	3.50 × 10^{-15}	6.52 × 10^{-2}
	$\tilde{x}$	4.65 × 10^{2}	0.995****	0.12	58.26	9.28 × 10^{2}****	3.55 × 10^{4}****	8.76 × 10^{5}	3.64 × 10^{-7}****	9.90 × 10^{3}	3.93 × 10^{-24}	9.40*
	Q_1	3.13 × 10^{2}	0.991	6.03 × 10^{-2}	36.11	3.36 × 10^{2}	1.30 × 10^{4}	2.47 × 10^{5}	6.97 × 10^{-8}	9.34 × 10^{3}	6.62 × 10^{-38}	9.10
	Q_3	6.91 × 10^{2}	0.998	0.20	79.48	2.38 × 10^{3}	1.62 × 10^{5}	2.92 × 10^{6}	2.80 × 10^{-6}	1.12 × 10^{4}	3.49 × 10^{-19}	9.80
	c_v	0.60	0.03	0.70	0.60	4.98	2.39	2.47	4.03	0.12	4.08	9.10
$\dot{k}_J = \dot{k}_M$	$\bar{x}$	6.75 × 10^{2}	0.762	0.14	63.29	1.25 × 10^{5}	2.64 × 10^{6}	8.02 × 10^{6}	6.31 × 10^{-3}	1.01 × 10^{4}	5.64 × 10^{-15}	9.22
	SE	60.41	2.66 × 10^{-2}	1.44 × 10^{-2}	6.11	4.17 × 10^{4}	1.49 × 10^{6}	5.47 × 10^{6}	6.10 × 10^{-4}	1.93 × 10^{2}	3.47 × 10^{-15}	6.53 × 10^{-2}
	$\tilde{x}$	6.24 × 10^{2}	0.804****	0.13	59.40	4.88 × 10^{4}****	7.23 × 10^{5}****	1.39 × 10^{6}	5.96 × 10^{-3}****	9.89 × 10^{3}	1.89 × 10^{-26}	9.10*
	Q_1	3.73 × 10^{2}	0.621	6.22 × 10^{-2}	34.88	1.15 × 10^{4}	1.25 × 10^{5}	2.11 × 10^{5}	3.31 × 10^{-3}	9.34 × 10^{3}	9.79 × 10^{-40}	9.00
	Q_3	9.62 × 10^{2}	0.906	0.19	80.25	1.03 × 10^{5}	1.65 × 10^{6}	3.63 × 10^{6}	8.35 × 10^{-3}	1.12 × 10^{4}	4.85 × 10^{-19}	9.60
	c_v	0.57	0.22	0.66	0.61	2.11	3.56	4.31	0.61	0.12	3.89	9.60

2.3.2 DEB parameters

The covariation method allowed us to estimate values for the entire set of relevant primary (core and auxiliary) (Table 2.9) and compound DEB parameters (Table 2.10). The rates obtained at the reference temperature were also converted to the corresponding values at each specific average adult body temperature (Table 2.11).

Considering the observed coefficients of variation (c_v) of all the metabolic rates at both the reference temperature and at each specific average adult body temperature, it is possible to observe how the short range of adult body temperatures (a difference of about 3.6 °C) hardly affects the variation levels observed at the reference temperature. The c_v of $\dot{v}^T$ is 1.5% lower than that of $\dot{v}$ and the c_v of $\dot{k}_J^T$ is 1.1% higher than that of $\dot{k}_J$. Taking this into consideration, we will focus our discussion on the values at the reference temperature for comparison purposes.

The parameter with the highest degree of variation was E_H^b and in fact the highest degrees of variation were observed in all the primary DEB parameters related with maturity. The primary DEB parameters corresponding to each maturity threshold, E_H^b, E_H^x and E_H^p, are expected to scale with body size, i.e., with the ultimate structural body length, L_∞ (cm). The variation observed regarding the cumulated energy invested in maturation up to hatching is higher than that observed for puberty and fledging. Fledging seems to be the life stage transition that is more stable across our sample of species.

The single parameter directly related only to the life span – $\ddot{h}_a$ – is also one of the parameters with a high coefficient of variation, naturally expressing the variation that exists in the life span of our sampled bird species.

The lowest degrees of variation were observed in a few of the core DEB primary parameters: κ, $[E_G]$, $[\dot{p}_M]$ and $\{\dot{p}_{Am}\}$; as well as in the DEB compound parameter $\dot{k}_M$.

All the parameters exhibit a left skew in the distribution of estimated values, except for the cases of κ and $[E_G]$, which practically do not exhibit any skew. This asymmetric distribution is particularly strong in those parameters that present large dispersion of values, i.e., E_H^b, $\ddot{h}_a$ and $\dot{k}_J$.

Table 2.9 – Estimated values for the main primary (core and auxiliary) DEB parameters at the reference temperature (T_{ref} = 293 K). The parameter abbreviations and their corresponding names are the following: δ_M – shape coefficient (-); $\{\dot{p}_{Am}\}$ – maximum specific assimilation rate (J d^{-1} cm^{-2}); κ – allocation fraction to soma (-); $\dot{v}$ – energy conductance (cm d^{-1}); $[\dot{p}_M]$ – volume-specific somatic maintenance rate (J d^{-1} cm^{-3}); E_H^b – maturity at birth (hatching) (J); E_H^x – maturity at fledging (J); E_H^p – maturity at puberty (J); $\dot{k}_J$ – maturity maintenance rate coefficient (d^{-1}); $[E_G]$ – specific cost for structure (J cm^{-3}); $\ddot{h}_a$ – Weibull ageing acceleration (d^{-2}). Statistical abbreviations are as follow: $\bar{x}$ – mean; SE – standard error; $\tilde{x}$ – median; Q_1 – lower quartile; Q_3 – upper quartile; c_v – coefficient of variation.

Species	δ_M (-)	$\{\dot{p}_{Am}\}$ (J d^{-1} cm^{-2})	κ (-)	$\dot{v}$ (cm d^{-1})	$[\dot{p}_M]$ (J d^{-1} cm^{-3})	E_H^b (J)	E_H^x (J)	E_H^p (J)	$\dot{k}_J$ (d^{-1})	$[E_G]$ (J cm^{-3})	$\ddot{h}_a$ (d^{-2})
Aquila chrysaetos	0.17	1.01×10^3	0.998	0.19	72.24	1.57×10^3	2.41×10^5	9.28×10^6	1.41×10^{-8}	1.10×10^4	7.47×10^{-33}
Anas platyrhynchos	0.16	3.40×10^2	0.989	9.36×10^{-2}	37.52	2.58×10^3	2.45×10^5	1.63×10^6	1.14×10^{-7}	8.59×10^3	3.50×10^{-26}
Apus apus	0.20	4.40×10^2	0.998	0.35	133.32	70.82	7.29×10^3	8.26×10^4	3.21×10^{-6}	1.12×10^4	9.77×10^{-90}
Bucorvus leadbeateri	0.11	6.33×10^2	0.999	6.11×10^{-2}	51.81	553.47	1.32×10^5	2.79×10^5	6.48×10^{-6}	1.09×10^4	1.93×10^{-26}
Podargus strigoides	0.16	7.20×10^2	0.998	0.25	100.30	271.24	1.77×10^4	2.15×10^5	3.11×10^{-5}	1.12×10^4	1.50×10^{-51}
Cariama cristata	0.14	6.25×10^2	0.998	0.14	50.58	1.08×10^3	2.87×10^4	7.73×10^5	4.45×10^{-6}	1.12×10^4	1.73×10^{-23}
Larus argentatus	0.14	6.35×10^2	0.996	0.11	74.54	2.23×10^3	1.27×10^5	6.89×10^7	2.37×10^{-9}	9.32×10^3	1.40×10^{-43}
Ciconia ciconia	0.11	1.44×10^3	0.998	0.24	115.10	1.07×10^3	4.47×10^5	7.22×10^7	1.85×10^{-7}	9.87×10^3	1.30×10^{-39}
Urocolius macrourus	0.32	3.55×10^2	0.991	0.20	97.76	199.33	4.55×10^3	1.11×10^5	9.66×10^{-7}	9.82×10^3	2.86×10^{-37}
Columba livia	0.19	4.90×10^2	0.994	0.18	78.64	1.03×10^3	6.43×10^4	3.95×10^5	1.17×10^{-7}	1.18×10^4	5.85×10^{-57}
Todiramphus cinnamominus	0.17	3.01×10^2	0.993	0.17	80.30	352.36	1.45×10^4	8.34×10^4	3.79×10^{-5}	8.86×10^3	3.36×10^{-33}
Cuculus canorus	0.14	6.05×10^2	0.998	0.31	133.27	46.50	6.37×10^3	4.99×10^4	2.59×10^{-6}	9.37×10^3	3.78×10^{-46}
Rhynochetos jubatus	0.15	5.52×10^2	0.991	0.15	60.63	5.63×10^3	4.53×10^5	1.22×10^6	2.48×10^{-4}	1.11×10^4	9.13×10^{-26}
Falco naumanni	0.16	9.51×10^2	0.997	0.43	189.99	314.03	2.83×10^4	4.00×10^5	3.29×10^{-7}	1.14×10^4	5.18×10^{-43}
Gallus gallus	0.15	2.37×10^2	0.963	4.41×10^{-2}	27.13	7.37×10^3	1.83×10^4	8.35×10^5	5.37×10^{-4}	9.93×10^3	6.48×10^{-18}
Gavia immer	0.17	7.75×10^2	0.998	0.16	55.88	990.75	1.79×10^5	1.38×10^6	7.43×10^{-8}	1.04×10^4	6.01×10^{-21}
Gallinula chloropus	0.18	3.30×10^2	0.983	0.10	53.74	1.64×10^3	1.11×10^5	9.61×10^5	1.36×10^{-6}	8.06×10^3	7.22×10^{-23}
Leptosomus discolor	0.11	83.56	0.993	1.16×10^{-2}	16.96	115.59	8.93×10^2	6.66×10^4	6.59×10^{-7}	8.89×10^3	8.95×10^{-15}
Mesitornis variegatus	0.13	1.15×10^2	0.993	2.39×10^{-2}	27.43	323.01	-	1.08×10^5	1.12×10^{-7}	1.18×10^4	6.41×10^{-15}
Tauraco erythrolophus	0.12	2.12×10^2	0.994	6.14×10^{-2}	36.28	874.92	9.40×10^3	1.80×10^5	3.99×10^{-7}	1.04×10^4	3.57×10^{-21}
Opisthocomus hoazin	0.12	3.25×10^2	0.997	9.14×10^{-2}	40.23	571.03	5.15×10^3	4.85×10^5	1.96×10^{-7}	9.36×10^3	4.87×10^{-23}
Ardeotis kori	0.14	3.34×10^2	0.998	3.10×10^{-2}	20.84	980.65	1.07×10^4	2.43×10^6	4.56×10^{-8}	9.40×10^3	4.68×10^{-15}

Parus major	0.18	3.51×10^{2}	0.991	0.27	139.73	98.44	7.52×10^{3}	2.05×10^{5}	7.04×10^{-7}	8.59×10^{3}	1.28×10^{-87}
Pelecanus onocrotalus	0.11	6.24×10^{2}	0.998	9.55×10^{-2}	35.93	1.24×10^{3}	1.62×10^{5}	3.15×10^{6}	3.67×10^{-8}	1.04×10^{4}	1.46×10^{-21}
Phaethon rubricauda	0.11	6.63×10^{2}	0.998	0.21	78.06	745.63	9.15×10^{4}	4.89×10^{5}	3.21×10^{-7}	9.39×10^{3}	1.97×10^{-37}
Phoeniconaias minor	0.12	5.90×10^{2}	0.998	0.16	55.50	1.17×10^{3}	1.31×10^{5}	2.24×10^{6}	3.35×10^{-6}	9.35×10^{3}	5.87×10^{-40}
Ramphastos toco	0.12	5.33×10^{2}	0.998	0.11	71.76	218.49	2.80×10^{4}	1.37×10^{6}	6.50×10^{-8}	8.78×10^{3}	7.76×10^{-24}
Podilymbus podiceps	0.20	3.57×10^{2}	0.994	0.13	51.25	777.15	4.99×10^{4}	5.64×10^{5}	3.01×10^{-6}	9.35×10^{3}	1.31×10^{-20}
Diomedea exulans	0.12	1.00×10^{3}	0.998	5.99×10^{-2}	67.75	4.84×10^{3}	1.66×10^{6}	1.83×10^{7}	1.63×10^{-8}	1.30×10^{4}	2.47×10^{-21}
Forpus passerinus	0.23	2.75×10^{2}	0.984	0.20	97.71	255.42	1.65×10^{4}	7.65×10^{4}	2.39×10^{-6}	8.59×10^{3}	6.32×10^{-73}
Pterocles alchata	0.18	2.64×10^{2}	0.996	8.29×10^{-2}	42.41	571.89	1.30×10^{4}	3.15×10^{5}	6.05×10^{-7}	1.17×10^{4}	4.84×10^{-29}
Pygoscelis adeliae	0.22	1.43×10^{3}	0.999	0.28	94.41	842.81	4.75×10^{4}	5.24×10^{6}	4.71×10^{-8}	1.31×10^{4}	9.06×10^{-20}
Tyto alba	0.17	4.30×10^{2}	0.980	6.06×10^{-2}	72.99	2.52×10^{3}	1.51×10^{5}	1.62×10^{6}	3.00×10^{-7}	1.09×10^{4}	6.08×10^{-19}
Phalacrocorax auritus	0.13	7.44×10^{2}	0.998	0.17	69.74	348.93	2.95×10^{4}	2.69×10^{6}	8.86×10^{-9}	8.89×10^{3}	5.32×10^{-27}
Euptilotis neoxenus	0.13	3.54×10^{2}	0.995	0.13	78.67	587.37	1.49×10^{4}	9.17×10^{5}	2.21×10^{-7}	8.77×10^{3}	1.31×10^{-37}
Apteryx mantelli	0.15	1.27×10^{2}	0.791	5.02×10^{-2}	8.20	5.77×10^{5}	1.01×10^{6}	4.47×10^{7}	2.54×10^{-5}	9.96×10^{3}	3.17×10^{-18}
Dromaius novaehollandiae	0.18	7.24×10^{2}	0.985	3.04×10^{-2}	29.06	2.48×10^{4}	3.55×10^{4}	3.30×10^{7}	1.61×10^{-6}	9.85×10^{3}	4.29×10^{-14}
Rhea americana	0.19	2.63×10^{2}	0.978	4.13×10^{-2}	10.55	5.46×10^{4}	2.63×10^{6}	1.61×10^{7}	2.39×10^{-6}	9.94×10^{3}	1.34×10^{-13}
Struthio camelus	0.17	9.07×10^{2}	0.993	4.99×10^{-2}	25.18	2.82×10^{4}	3.36×10^{6}	1.35×10^{8}	1.93×10^{-8}	1.12×10^{4}	5.57×10^{-15}
Rhynchotus rufescens	0.19	2.23×10^{2}	0.986	3.97×10^{-2}	28.63	3.95×10^{3}	7.92×10^{3}	5.86×10^{5}	5.57×10^{-8}	9.85×10^{3}	1.42×10^{-14}
$\bar{x}$	0.16	5.34×10^{2}	0.988	0.14	65.30	1.83×10^{4}	2.97×10^{5}	1.07×10^{7}	2.29×10^{-5}	1.01×10^{4}	5.43×10^{-15}
SE	6.59×10^{-3}	50.88	5.19×10^{-3}	1.55×10^{-2}	6.22	1.44×10^{4}	1.13×10^{5}	4.19×10^{6}	1.46×10^{-5}	1.93×10^{2}	3.50×10^{-15}
$\tilde{x}$	0.16	4.65×10^{2}	0.995	0.12	58.26	9.28×10^{2}	3.55×10^{4}	8.76×10^{5}	3.64×10^{-7}	9.90×10^{3}	3.93×10^{-24}
Q_1	0.13	3.13×10^{2}	0.991	6.03×10^{-2}	36.11	3.36×10^{2}	1.30×10^{4}	2.47×10^{5}	6.97×10^{-8}	9.34×10^{3}	6.62×10^{-38}
Q_3	0.18	6.91×10^{2}	0.998	0.20	79.48	2.38×10^{3}	1.62×10^{5}	2.92×10^{6}	2.80×10^{-6}	1.12×10^{4}	3.49×10^{-19}
c_v	0.26	0.60	0.03	0.70	0.60	4.98	2.39	2.47	4.03	0.12	4.08

Table 2.10 – Estimated values for the main compound DEB parameters and additional properties at the reference temperature (T_{ref} = 293 K). The parameter abbreviations and their corresponding names are the following: z – zoom factor (-); g – energy investment ratio (-); $\dot{k}_M$ – somatic maintenance rate coefficient (d^{-1}); $[E_m]$ – maximum reserve capacity (J cm^{-3}); $\dot{r}_B$ – von Bertalanffy growth rate (d^{-1}); $-J_O / W_d$ – dry mass-specific respiration (L g^{-1} h^{-1}); t_s – fasting capacity (d); W_w^m / L_∞^3 – maximum wet weight per ultimate structural volume (g cm^{-3}); M_E^0 – initial egg mass (C-mol); $\dot{p}_R^m / L_m^3$ – specific allocation to reproduction per maximum structural volume (J d^{-1} cm^{-3}); $\dot{p}_J^p / L_m^3$ – maturity maintenance at puberty per maximum structural volume (J d^{-1} cm^{-3}). Statistical abbreviations are as follow: $\bar{x}$ – mean; SE – standard error; $\tilde{x}$ – median; Q_1 – lower quartile; Q_3 – upper quartile; c_v – coefficient of variation.

Species	z (-)	g (-)	$\dot{k}_M$ (d^{-1})	$[E_m]$ (J cm^{-3})	$\dot{r}_B$ (d^{-1})	$-J_O / W_d$ (L g^{-1} h^{-1})	t_s (d)	W_w^m / L_∞^3 (g cm^{-3})	M_E^0 (C-mol)	$\dot{p}_R^m / L_m^3$ (J d^{-1} cm^{-3})	$\dot{p}_J^p / L_m^3$ (J d^{-1} cm^{-3})
Aquila chrysaetos	14.01	2.11	6.58×10^{-3}	5.21×10^{3}	1.49×10^{-3}	2.29×10^{-4}	2.00×10^{2}	1.54	2.29	0.13	4.75×10^{-5}
Anas platyrhynchos	8.96	2.39	4.37×10^{-3}	3.63×10^{3}	1.03×10^{-3}	1.58×10^{-4}	28.61	1.48	0.56	0.43	2.57×10^{-4}
Apus apus	3.29	8.96	1.19×10^{-2}	1.25×10^{3}	3.58×10^{-3}	5.58×10^{-4}	91.19	1.13	6.39×10^{-2}	0.29	7.43×10^{-3}
Bucorvus leadbeateri	12.21	1.05	4.75×10^{-3}	1.04×10^{4}	8.13×10^{-4}	1.20×10^{-4}	75.12	2.07	1.17	7.65×10^{-2}	9.95×10^{-4}
Podargus strigoides	7.16	3.92	8.94×10^{-3}	2.87×10^{3}	2.37×10^{-3}	3.68×10^{-4}	51.75	1.29	0.31	0.18	1.82×10^{-2}
Cariama cristata	12.33	2.43	4.52×10^{-3}	4.61×10^{3}	1.07×10^{-3}	1.64×10^{-4}	17.83	1.47	1.33	9.95×10^{-2}	1.83×10^{-3}
Larus argentatus	8.48	1.67	7.99×10^{-3}	5.60×10^{3}	1.67×10^{-3}	2.53×10^{-4}	34.52	1.68	1.33	0.33	2.68×10^{-4}
Ciconia ciconia	12.52	1.66	1.17×10^{-2}	5.96×10^{3}	2.43×10^{-3}	3.65×10^{-4}	21.84	1.68	1.42	0.23	6.82×10^{-3}
Urocolius macrourus	3.60	5.69	9.95×10^{-3}	1.74×10^{3}	2.82×10^{-3}	4.38×10^{-4}	14.65	1.20	4.56×10^{-2}	0.90	2.31×10^{-3}
Columba livia	6.19	4.36	6.69×10^{-3}	2.71×10^{3}	1.81×10^{-3}	2.83×10^{-4}	59.05	1.26	0.36	0.50	1.95×10^{-4}
Todiramphus cinnamominus	3.72	5.09	9.06×10^{-3}	1.75×10^{3}	2.52×10^{-3}	3.92×10^{-4}	11.54	1.22	0.10	0.52	6.11×10^{-2}
Cuculus canorus	4.53	4.81	1.42×10^{-2}	1.95×10^{3}	3.92×10^{-3}	6.11×10^{-4}	1.98×10^{2}	1.24	4.74×10^{-2}	0.28	1.39×10^{-3}
Rhynochetos jubatus	9.02	3.14	5.44×10^{-3}	3.58×10^{3}	1.38×10^{-3}	2.13×10^{-4}	85.53	1.36	1.40	0.16	0.41
Falco naumanni	4.99	5.21	1.67×10^{-2}	2.19×10^{3}	4.66×10^{-3}	7.22×10^{-4}	60.20	1.22	0.24	0.53	1.06×10^{-3}
Gallus gallus	8.41	1.92	2.73×10^{-3}	5.37×10^{3}	5.99×10^{-4}	9.45×10^{-5}	4.24×10^{2}	1.61	0.54	0.28	0.75
Gavia immer	13.85	2.18	5.38×10^{-3}	4.78×10^{3}	1.23×10^{-3}	1.86×10^{-4}	1.76×10^{2}	1.52	1.63	8.59×10^{-2}	3.85×10^{-5}
Gallinula chloropus	6.04	2.53	6.67×10^{-3}	3.24×10^{3}	1.59×10^{-3}	2.42×10^{-4}	94.97	1.45	0.23	0.93	5.91×10^{-3}
Leptosomus discolor	4.89	1.25	1.91×10^{-3}	7.19×10^{3}	3.53×10^{-4}	5.25×10^{-5}	88.58	1.92	5.20×10^{-2}	0.11	3.74×10^{-4}
Mesitornis variegatus	4.18	2.45	2.33×10^{-3}	4.83×10^{3}	5.52×10^{-4}	8.61×10^{-5}	5.17×10^{2}	1.46	0.12	0.18	1.65×10^{-4}
Tauraco erythrolophus	5.80	3.04	3.48×10^{-3}	3.45×10^{3}	8.74×10^{-4}	1.33×10^{-4}	9.36	1.37	0.32	0.23	3.68×10^{-4}

Opisthocomus hoazin	8.06	2.64	4.30×10^{-3}	3.56×10^{3}	1.04×10^{-3}	1.59×10^{-4}	1.82×10^{2}	1.43	0.41	0.14	1.81×10^{-4}
Ardeotis kori	15.97	0.87	2.22×10^{-3}	1.08×10^{4}	3.45×10^{-4}	5.12×10^{-5}	40.03	2.30	1.80	3.90×10^{-2}	2.71×10^{-5}
Parus major	2.49	6.63	1.63×10^{-2}	1.31×10^{3}	4.71×10^{-3}	7.40×10^{-4}	66.02	1.17	2.24×10^{-2}	1.27	9.40×10^{-3}
Pelecanus onocrotalus	17.33	1.60	3.44×10^{-3}	6.53×10^{3}	7.06×10^{-4}	1.06×10^{-4}	69.17	1.71	2.14	5.78×10^{-2}	2.22×10^{-5}
Phaethon rubricauda	8.48	3.01	8.31×10^{-3}	3.13×10^{3}	2.08×10^{-3}	3.19×10^{-4}	52.89	1.38	1.04	0.13	2.57×10^{-4}
Phoeniconaias minor	10.62	2.56	5.94×10^{-3}	3.66×10^{3}	1.42×10^{-3}	2.17×10^{-4}	2.46×10^{2}	1.44	1.63	8.88×10^{-2}	6.29×10^{-3}
Ramphastos toco	7.41	1.77	8.17×10^{-3}	4.96×10^{3}	1.74×10^{-3}	2.63×10^{-4}	13.85	1.63	0.28	0.15	2.19×10^{-4}
Podilymbus podiceps	6.92	3.47	5.48×10^{-3}	2.71×10^{3}	1.42×10^{-3}	2.18×10^{-4}	74.93	1.33	0.28	0.32	5.13×10^{-3}
Diomedea exulans	14.75	0.78	5.20×10^{-3}	1.67×10^{4}	7.61×10^{-4}	1.13×10^{-4}	54.38	2.45	10.39	0.10	9.27×10^{-5}
Forpus passerinus	2.77	6.45	1.14×10^{-2}	1.35×10^{3}	3.28×10^{-3}	5.11×10^{-4}	97.22	1.17	3.31×10^{-2}	1.57	8.58×10^{-3}
Pterocles alchata	6.19	3.71	3.62×10^{-3}	3.18×10^{3}	9.49×10^{-4}	1.47×10^{-4}	63.80	1.31	0.33	0.17	8.05×10^{-4}
Pygoscelis adeliae	15.12	2.54	7.23×10^{-3}	5.13×10^{3}	1.73×10^{-3}	2.65×10^{-4}	35.85	1.45	2.05	9.44×10^{-2}	7.15×10^{-5}
Tyto alba	5.78	1.56	6.72×10^{-3}	7.10×10^{3}	1.37×10^{-3}	2.04×10^{-4}	3.08×10^{2}	1.73	0.34	1.49	2.52×10^{-3}
Phalacrocorax auritus	10.66	2.00	7.85×10^{-3}	4.45×10^{3}	1.74×10^{-3}	2.66×10^{-4}	8.19×10^{2}	1.57	0.59	0.11	1.97×10^{-5}
Euptilotis neoxenus	4.48	3.13	8.97×10^{-3}	2.82×10^{3}	2.26×10^{-3}	3.47×10^{-4}	6.04×10^{2}	1.36	0.27	0.39	2.25×10^{-3}
Apteryx mantelli	12.22	4.99	8.23×10^{-4}	2.52×10^{3}	2.29×10^{-4}	3.52×10^{-5}	7.22×10^{2}	1.29	5.89	1.55	0.62
Dromaius novaehollandiae	24.54	0.42	2.95×10^{-3}	2.38×10^{4}	2.91×10^{-4}	4.15×10^{-5}	1.96×10^{2}	3.72	7.89	0.44	3.59×10^{-3}
Rhea americana	24.37	1.60	1.06×10^{-3}	6.37×10^{3}	2.17×10^{-4}	3.18×10^{-5}	2.00×10^{2}	1.73	7.02	0.23	2.65×10^{-3}
Struthio camelus	35.78	0.62	2.25×10^{-3}	1.82×10^{4}	2.87×10^{-4}	4.23×10^{-5}	28.61	2.84	17.24	0.17	5.67×10^{-5}
Rhynchotus rufescens	7.68	1.78	2.91×10^{-3}	5.62×10^{3}	6.20×10^{-4}	9.28×10^{-5}	91.19	1.64	0.73	0.41	7.19×10^{-5}
$\bar{x}$	9.90	2.95	6.51×10^{-3}	5.40×10^{3}	1.60×10^{-3}	2.46×10^{-4}	152.05	1.60	1.85	0.38	4.85×10^{-2}
SE	1.07	0.29	6.23×10^{-4}	7.42×10^{-2}	1.85×10^{-4}	2.89×10^{-5}	31.19	7.86×10^{-2}	0.54	6.64×10^{-2}	2.58×10^{-2}
$\tilde{x}$	8.24	2.49	5.71×10^{-3}	4.06×10^{3}	1.40×10^{-3}	2.15×10^{-4}	73.54	1.46	0.55	0.23	1.03×10^{-3}
Q_1	5.39	1.67	3.46×10^{-3}	2.77×10^{3}	7.33×10^{-4}	1.10×10^{-4}	37.94	1.30	0.25	0.12	1.73×10^{-4}
Q_3	12.42	3.81	8.63×10^{-3}	5.79×10^{3}	2.17×10^{-3}	3.33×10^{-4}	188.98	1.68	1.63	0.43	6.10×10^{-3}
c_v	0.68	0.63	0.60	0.87	0.73	0.74	1.3	0.31	1.84	1.09	3.36

Table 2.11 – Estimated values for selected primary and compound DEB parameters at each specific average adult body temperature (T_{am}). The parameter abbreviations and their corresponding names are the following: $\{\dot{p}_{Am}^T\}$ – maximum surface-specific assimilation rate (J d^{-1} cm^{-2}); $\dot{v}^T$ – energy conductance (cm d^{-1}); $[\dot{p}_M^T]$ – volume-specific somatic maintenance rate (J d^{-1} cm^{-3}); $\dot{k}_J^T$ – maturity maintenance rate coefficient (d^{-1}); $\dot{k}_M^T$ – somatic maintenance rate coefficient (d^{-1}); $\dot{r}_B^T$ – von Bertalanffy growth rate (d^{-1}); -J_O^T / W_d – dry mass-specific respiration (L g^{-1} h^{-1}); t_s^T – fasting capacity (d). Statistical abbreviations are as follow: $\bar{x}$ – mean; SE – standard error; $\tilde{x}$ – median; Q_1 – lower quartile; Q_3 – upper quartile; c_v – coefficient of variation.

Species	$\{\dot{p}_{Am}^T\}$ (J d^{-1} cm^{-2})	$\dot{v}^T$ (cm d^{-1})	$[\dot{p}_M^T]$ (J d^{-1} cm^{-3})	$\dot{k}_J^T$ (d^{-1})	$\dot{k}_M^T$ (d^{-1})	$\dot{r}_B^T$ (d^{-1})	-J_O^T / W_d (L g^{-1} h^{-1})	t_s^T (d)
Aquila chrysaetos	2.13 × 10^4	4.08	1.52 × 10^3	2.95 × 10^{-7}	0.14	3.12 × 10^{-2}	4.80 × 10^{-3}	3.44
Anas platyrhynchos	1.08 × 10^4	2.96	1.19 × 10^3	3.59 × 10^{-6}	0.14	3.25 × 10^{-2}	5.00 × 10^{-3}	3.06
Apus apus	9.94 × 10^3	7.96	3.01 × 10^3	7.26 × 10^{-5}	0.27	8.09 × 10^{-2}	1.26 × 10^{-2}	0.41
Bucorvus leadbeateri	1.69 × 10^4	1.63	1.39 × 10^3	1.74 × 10^{-4}	0.13	2.17 × 10^{-2}	3.20 × 10^{-3}	7.48
Podargus strigoides	1.35 × 10^4	4.71	1.88 × 10^3	5.84 × 10^{-4}	0.17	4.46 × 10^{-2}	6.90 × 10^{-3}	1.52
Cariama cristata	1.41 × 10^4	3.06	1.14 × 10^3	1.01 × 10^{-4}	0.10	2.41 × 10^{-2}	3.70 × 10^{-3}	4.04
Larus argentatus	2.01 × 10^4	3.59	2.36 × 10^3	7.50 × 10^{-8}	0.25	5.28 × 10^{-2}	8.00 × 10^{-3}	2.37
Ciconia ciconia	3.52 × 10^4	5.91	2.81 × 10^3	4.52 × 10^{-6}	0.28	5.92 × 10^{-2}	8.90 × 10^{-3}	2.12
Urocolius macrourus	9.16 × 10^3	5.26	2.52 × 10^3	2.49 × 10^{-5}	0.26	7.29 × 10^{-2}	1.13 × 10^{-2}	0.69
Columba livia	1.42 × 10^4	5.24	2.28 × 10^3	3.40 × 10^{-6}	0.19	5.26 × 10^{-2}	8.20 × 10^{-3}	1.19
Todiramphus cinnamominus	7.46 × 10^3	4.26	1.99 × 10^3	9.38 × 10^{-4}	0.22	6.25 × 10^{-2}	9.70 × 10^{-3}	0.88
Cuculus canorus	1.59 × 10^4	8.17	3.51 × 10^3	6.82 × 10^{-5}	0.38	0.10	1.61 × 10^{-2}	0.56
Rhynochetos jubatus	1.04 × 10^4	2.89	1.14 × 10^3	4.66 × 10^{-3}	0.10	2.58 × 10^{-2}	4.00 × 10^{-3}	3.15
Falco naumanni	2.15 × 10^4	9.80	4.29 × 10^3	7.44 × 10^{-6}	0.38	0.11	1.63 × 10^{-2}	0.51
Gallus gallus	7.27 × 10^3	1.35	8.32 × 10^2	1.65 × 10^{-2}	8.38 × 10^{-2}	1.84 × 10^{-2}	2.90 × 10^{-3}	6.45
Gavia immer	1.75 × 10^4	3.67	1.26 × 10^3	1.68 × 10^{-6}	0.12	2.77 × 10^{-2}	4.20 × 10^{-3}	3.79
Gallinula chloropus	8.18 × 10^3	2.53	1.33 × 10^3	3.36 × 10^{-5}	0.17	3.95 × 10^{-2}	6.00 × 10^{-3}	2.43
Leptosomus discolor	2.07 × 10^3	0.29	4.20 × 10^2	1.63 × 10^{-5}	4.73 × 10^{-2}	8.70 × 10^{-3}	1.30 × 10^{-3}	17.11
Mesitornis variegatus	3.35 × 10^3	0.69	7.96 × 10^2	3.25 × 10^{-6}	6.77 × 10^{-2}	1.60 × 10^{-2}	2.50 × 10^{-3}	6.07
Tauraco erythrolophus	4.78 × 10^3	1.39	8.20 × 10^2	9.01 × 10^{-6}	7.87 × 10^{-2}	1.97 × 10^{-2}	3.00 × 10^{-3}	4.20

Opisthocomus hoazin	7.35×10^{3}	2.06	9.09×10^{2}	4.43×10^{-6}	9.71×10^{-2}	2.35×10^{-2}	3.60×10^{-3}	3.92
Ardeotis kori	9.13×10^{3}	0.85	5.70×10^{2}	1.25×10^{-6}	6.07×10^{-2}	9.40×10^{-3}	1.40×10^{-3}	18.88
Parus major	1.08×10^{4}	8.23	4.29×10^{3}	2.16×10^{-5}	0.50	0.15	2.27×10^{-2}	0.30
Pelecanus onocrotalus	1.41×10^{4}	2.16	8.12×10^{2}	8.30×10^{-7}	7.77×10^{-2}	1.60×10^{-2}	2.40×10^{-3}	8.04
Phaethon rubricauda	1.39×10^{4}	4.46	1.64×10^{3}	6.75×10^{-6}	0.18	4.37×10^{-2}	6.70×10^{-3}	1.91
Phoeniconaias minor	1.44×10^{4}	3.93	1.35×10^{3}	8.18×10^{-5}	0.15	3.47×10^{-2}	5.30×10^{-3}	2.71
Ramphastos toco	1.18×10^{4}	2.37	1.58×10^{3}	1.44×10^{-6}	0.18	3.85×10^{-2}	5.80×10^{-3}	3.13
Podilymbus podiceps	8.84×10^{3}	3.26	1.27×10^{3}	7.46×10^{-5}	0.14	3.51×10^{-2}	5.40×10^{-3}	2.13
Diomedea exulans	2.48×10^{4}	1.48	1.68×10^{3}	4.03×10^{-7}	0.13	1.88×10^{-2}	2.80×10^{-3}	9.95
Forpus passerinus	6.03×10^{3}	4.45	2.14×10^{3}	5.24×10^{-5}	0.25	7.19×10^{-2}	1.12×10^{-2}	0.63
Pterocles alchata	8.59×10^{3}	2.70	1.38×10^{3}	1.97×10^{-5}	0.12	3.10×10^{-2}	4.80×10^{-3}	2.30
Pygoscelis adeliae	2.85×10^{4}	5.56	1.88×10^{3}	9.40×10^{-7}	0.14	3.46×10^{-2}	5.30×10^{-3}	2.72
Tyto alba	9.72×10^{3}	1.37	1.65×10^{3}	6.78×10^{-6}	0.15	3.09×10^{-2}	4.60×10^{-3}	4.30
Phalacrocorax auritus	2.18×10^{4}	4.91	2.04×10^{3}	2.60×10^{-7}	0.23	5.11×10^{-2}	7.80×10^{-3}	2.18
Euptilotis neoxenus	8.78×10^{3}	3.11	1.95×10^{3}	5.47×10^{-6}	0.22	5.61×10^{-2}	8.60×10^{-3}	1.45
Apteryx mantelli	2.52×10^{3}	1.00	1.63×10^{2}	5.05×10^{-4}	1.64×10^{-2}	4.50×10^{-3}	7.00×10^{-4}	15.48
Dromaius novaehollandiae	1.40×10^{4}	0.59	5.61×10^{2}	3.10×10^{-5}	5.69×10^{-2}	5.60×10^{-3}	8.00×10^{-4}	42.42
Rhea americana	6.61×10^{3}	1.04	2.65×10^{2}	6.01×10^{-5}	2.67×10^{-2}	5.50×10^{-3}	8.00×10^{-4}	23.99
Struthio camelus	1.93×10^{4}	1.06	5.37×10^{2}	4.11×10^{-7}	4.80×10^{-2}	6.10×10^{-3}	9.00×10^{-4}	33.88
Rhynchotus rufescens	5.53×10^{3}	0.98	7.09×10^{2}	1.38×10^{-6}	7.20×10^{-2}	1.54×10^{-2}	2.30×10^{-3}	7.92
$\bar{x}$	1.28×10^{4}	3.38	1.60×10^{3}	6.01×10^{-4}	0.16	3.94×10^{-2}	6.06×10^{-3}	6.49
SE	1.13×10^{3}	0.37	155.46	4.24×10^{-4}	1.63×10^{-2}	4.80×10^{-3}	7.51×10^{-4}	1.45
$\tilde{x}$	1.08×10^{4}	3.01	1.38×10^{3}	8.22×10^{-6}	0.14	3.19×10^{-2}	4.75×10^{-3}	3.10
Q_1	7.82×10^{3}	1.38	826.11	1.56×10^{-6}	8.13×10^{-2}	1.86×10^{-2}	8.10×10^{-3}	1.72
Q_3	1.64×10^{4}	4.58	2.02×10^{3}	7.04×10^{-5}	0.22	5.27×10^{-2}	2.85×10^{-3}	6.96
c_v	0.56	0.69	0.62	4.46	0.64	0.77	0.78	1.41

2.3.3 Primary patterns

2.3.3.1 Maximum specific assimilation rate ($\{\dot{p}_{Am}\}$, J d^{-1} cm^{-2})

The maximum specific assimilation rate ($\{\dot{p}_{Am}\}$, J d^{-1} cm^{-2}) is expected to increase with increasing L_∞ and the values estimated for birds seem to follow this pattern. Most of the scatter beyond the effect of body size remains to be explained. However, most species exhibit values above the expectations obtained from the generalized animal, illustrating the generally high assimilation demand pattern of birds (Figure 2.1).

Four species exhibit values below these expectations. These include the Greater Rhea, the North Island Brown Kiwi, the Cuckoo Roller and the Kori Bustard. In the case of the first two, these low assimilation rates align with the slow somatic growth observed in some members of the Palaeognathae. If we compare the Greater Rhea, which reaches a wet weight of about 20 kg in about 400 days since hatching, with the Emu, another Palaeognathae with a similar length but which reaches approximately the double of the wet weight in the same amount of time, we understand why the first one does not require such a high assimilation rate as the second one. A similar comparison could be made between the Kori Bustard and the Adélie Penguin, with the second, despite slightly smaller, exhibiting a much higher assimilation rate and reaching about the double of the wet weight than the first, in about a month since hatching. The value estimated for the Cuckoo Roller is also slightly below the expected from the generalized animal. However, the value estimated for this species may be an underestimation driven by the fact that no post-hatching growth curve was available, i.e., the data from the incubation period dominated the parameterization process and no post-hatching acceleration of growth – such as that which is observed for most bird species – influenced the estimation procedure.

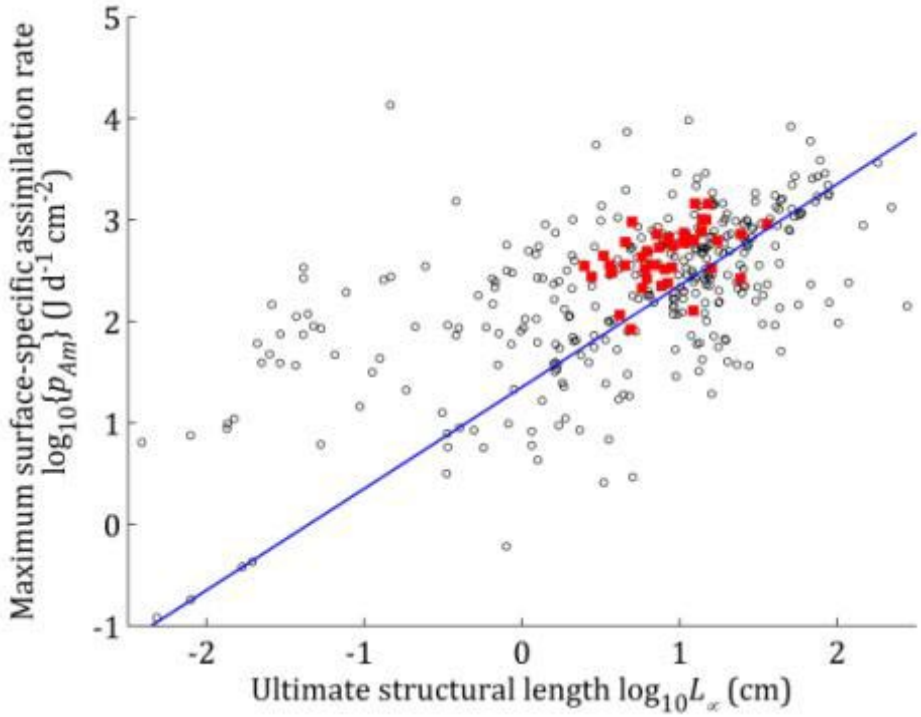

Figure 2.1 – Log-log plot of the maximum specific assimilation rate ($\{\dot{p}_{Am}\}$, J d^{-1} cm^{-2}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. Marker codes: squares – bird species; circles – other organisms from the "Add_my_pet" library. The line represents the expected values according to the generalized animal.

2.3.3.2 Allocation fraction to soma (κ, -)

The average allocation fraction to soma (*κ*, -) considering the whole collection of sampled bird species, is very high (0.988), with a very low coefficient of variation (0.03) (Table 2.9) despite the cases of the North Island Brown Kiwi (*Apteryx mantelli*) and the Red Junglefowl (*Gallus gallus*) that stand out has having the lowest *κ* values of 0.79 and 0.96, respectively. Only the value estimated for the Kiwi is at level of the expected values obtained from the generalized animal but the reason for this result does not rely on the pseudo-data – the Kiwi lays two clutches every year with three eggs that can reach a weight of approximately 20% of the average adult body weight each and the amount of energy invested in maturation up to fledging is among the highest of our sample (about a third of that estimated for the Ostrich) despite its small size of about 2.4 kg. The Kiwi also takes almost three years to reach the adult size. This parameter is not expected to scale with body size but a very slight positive trend is observable within the narrow range of values in which most of the estimated values are included (Figure 2.2).

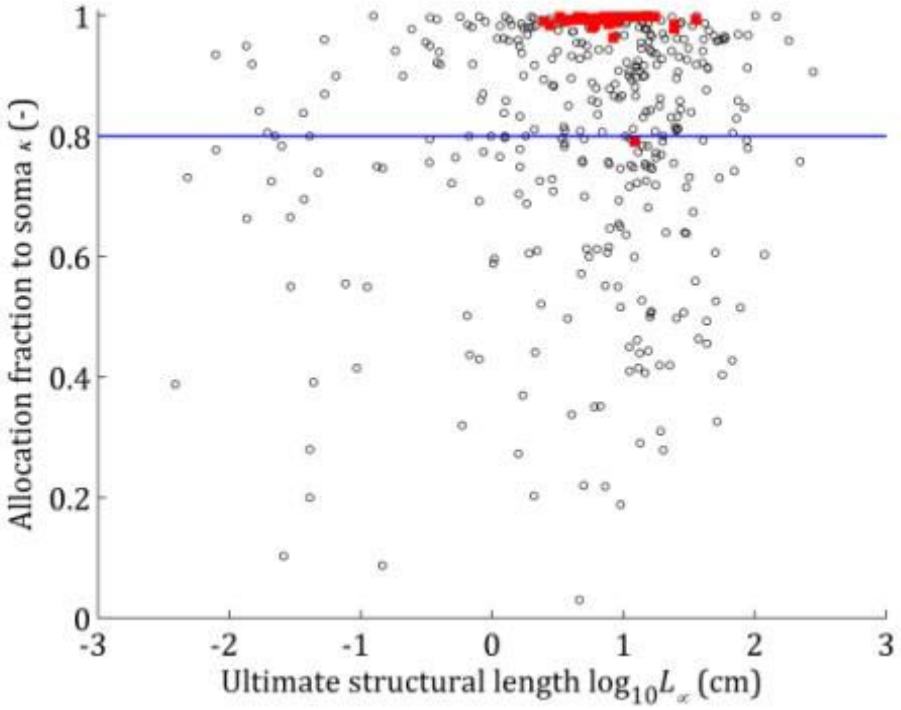

Figure 2.2 – The allocation fraction to soma (*κ*, -) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. Marker codes: squares – bird species; circles – other organisms from the "Add_my_pet" library. The line represents the expected values according to the generalized animal.

2.3.3.3 Energy conductance ($\dot{v}$, cm d^{-1})

The energy conductance ($\dot{v}$, cm d^{-1}) is expected to be independent of body size but there seems to be a decline occurring as L_∞ increases, although with considerable scatter. Most of the bird species exhibit values above the expectation from the generalized animal, except the Cuckoo Roller but, just as we observed regarding $\{\dot{p}_{Am}\}$, the value estimated for this species may be an underestimation driven by the absence of post-hatching growth data. Placed just slightly above the expected value for the generalized animal is the estimated value for the White-breasted Mesite – the other species in our sample for which no post-hatching growth data was available. The estimated values for these two species are also clearly deviated from the pattern (Figure 2.3).

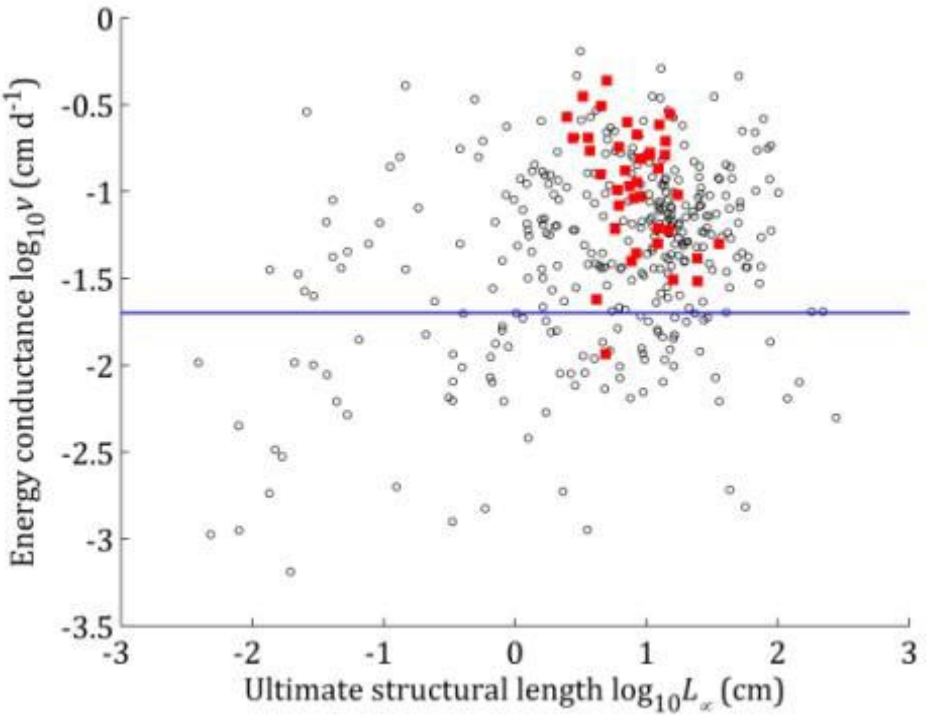

Figure 2.3 – Log-log plot of the energy conductance ($\dot{v}$, cm d^{-1}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. Marker codes: squares – bird species; circles – other organisms from the "Add_my_pet" library. The line represents the expected values according to the generalized animal.

2.3.3.4 Volume-specific somatic maintenance rate ([$\dot{p}_M$], J d^{-1} cm^{-3})

The volume-specific somatic maintenance rate ([$\dot{p}_M$], J d^{-1} cm^{-3}) is another parameter that is not expected to scale with body size. However, as L_∞ increases there seems to be a similar decline in [$\dot{p}_M$] as observed with $\dot{v}$, also with considerable scatter. Most of the values are scattered above the expected values from the generalized animal, except for the Greater Rhea, the North Island Brown Kiwi and the Cuckoo Roller. These three species also exhibited lower {$\dot{p}_{Am}$} values and the same considerations presented for that parameter apply to [$\dot{p}_M$] (Figure 2.4).

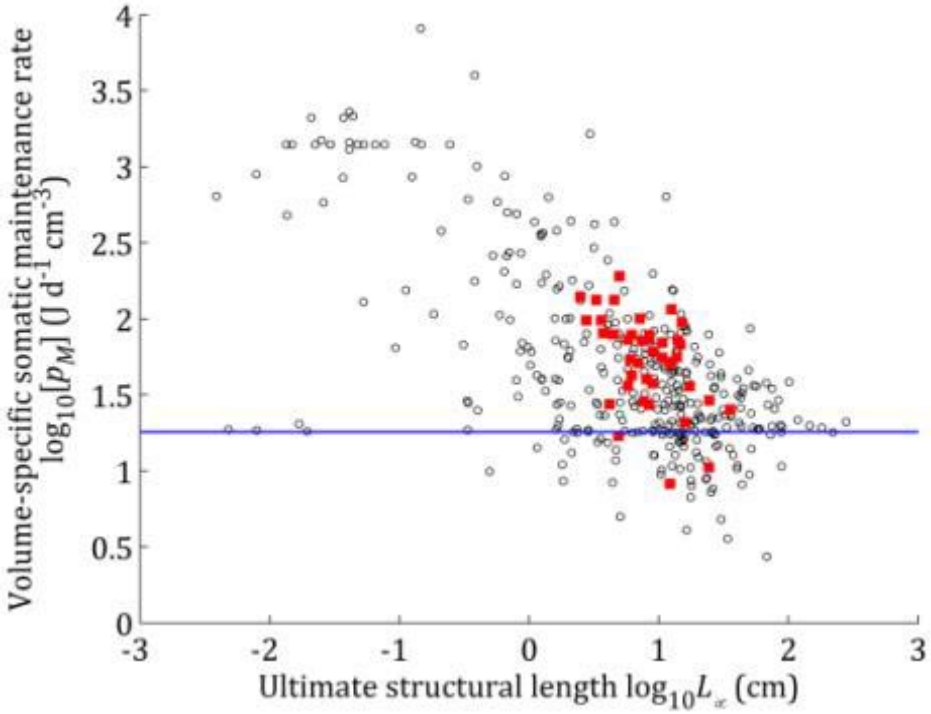

Figure 2.4 – Log-log plot of the volume-specific somatic maintenance rate ([$\dot{p}_M$], J d^{-1} cm^{-3}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. Marker codes: squares – bird species; circles – other organisms from the "Add_my_pet" library. The line represents the expected values according to the generalized animal.

2.3.3.5 Maturity at birth (hatching) (E_H^b, J)

The maturity at birth (E_H^b, J) is proportional to L_∞^3 and birds follow this pattern with little scatter. The estimated value for the Northern Island Brown Kiwi stands out as higher than expected for its size. Nevertheless, all the values are aligned with or somewhat above the expectations from the generalized animal (Figure 2.5).

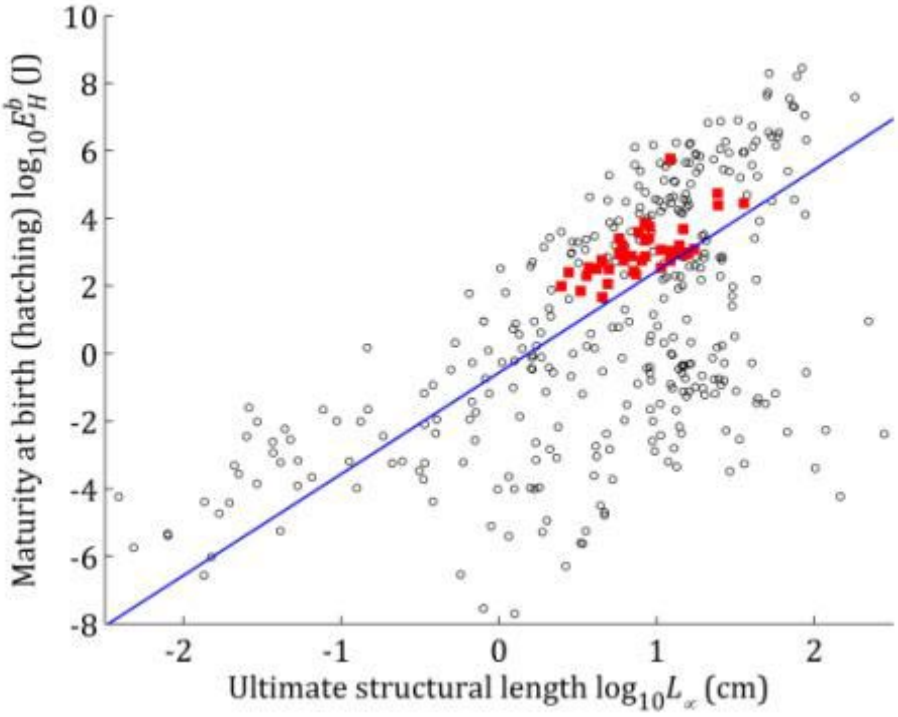

Figure 2.5 – Log-log plot of the maturity at birth (E_H^b, J) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. Marker codes: squares – bird species; circles – other organisms from the "Add_my_pet" library. The line represents the expected values according to the generalized animal.

2.3.3.6 Maturity at fledging (E_H^x, J)

Regarding the maturity at fledging (E_H^x, J), these values could not be compared to those estimated for other organisms considering that this particular stage of development is characteristic to birds' life history. This primary DEB parameter is expected to scale with L_∞^3 and the pattern follows these expectations (Figure 2.6).

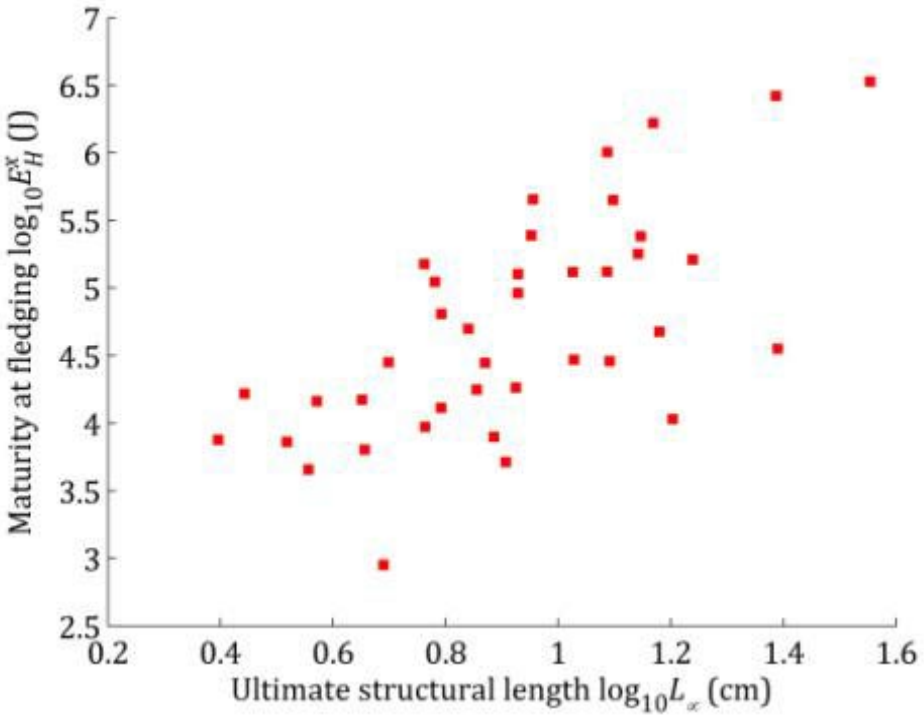

Figure 2.6 – Log-log plot of the maturity at fledging (E_H^x, J) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K.

2.3.3.7 Maturity at puberty (E_H^p, J)

The maturity at puberty (E_H^p, J) estimated values increased with increasing L_∞^3, as expected, and all the values were concentrated above the expectations from the generalized animal except in the case of the Southern Ground Hornbill which is aligned exactly with these expectations. Four species stand out as having energy investments in maturity up to puberty which are visibly higher than those expected from their body size: the Herring Gull, the European White Stork, the North Island Brown Kiwi and the Wandering Albatross. Shared by these three species are the particularly long periods of time that occur before the first reproductive event averaging 3, 4, 2.5 and 6 years, respectively (Figure 2.7).

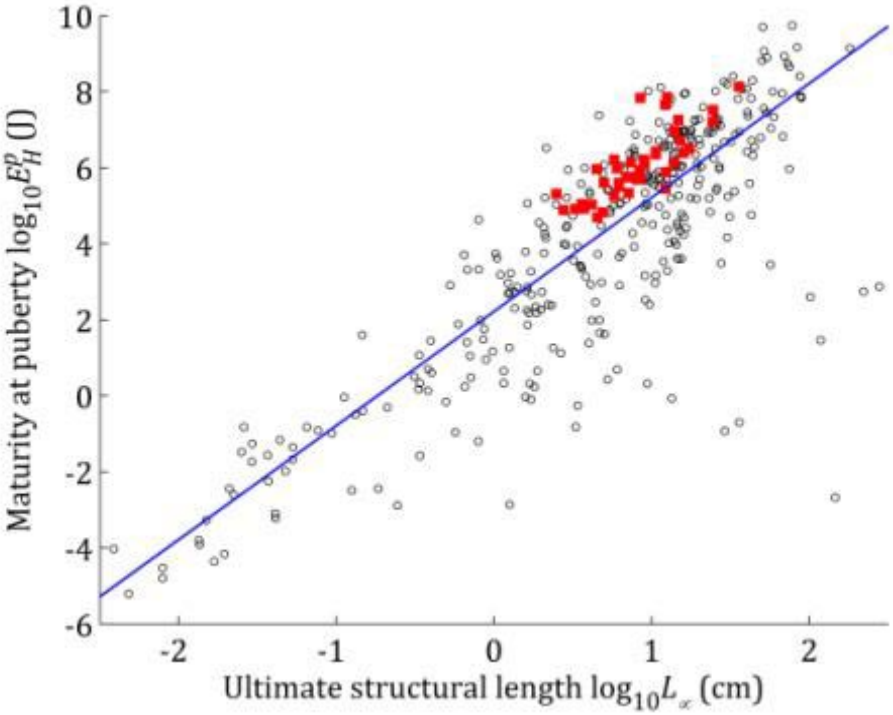

Figure 2.7 – Log-log plot of the maturity at puberty (E_H^p, J) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. Marker codes: squares – bird species; circles – other organisms from the "Add_my_pet" library. The line represents the expected values according to the generalized animal.

2.3.3.8 Maturity maintenance rate coefficient ($\dot{k}_J$, d^{-1})

The maturity maintenance rate coefficient ($\dot{k}_J$, d^{-1}) is expected to be independent from body size. The values obtained for birds regarding this parameter seem to be declining with L_∞ but with considerable scatter. What stands out is the fact that contrary to most other species present in the library, for which these values are close to or equal to the expectation from the generalized animal (revealing a possible strong effect of the pseudo-data), the estimated values for our sample of birds are considerably lower, distributing themselves between 2.4×10^{-9} for the Herring gull and 5.4×10^{-4} for the Red Junglefowl. The determinant factor for this range of values seems to be the fact that for most species of birds the wet weight converges to the average adult body size much sooner than the first reproduction occurs (and sexual puberty is mostly based on this last observation). The quick post-hatching growth of the soma and the energy requirements for maturity may be jointly constraining the value of the maintenance rate so as to allow an optimized use of energy (Figure 2.8).

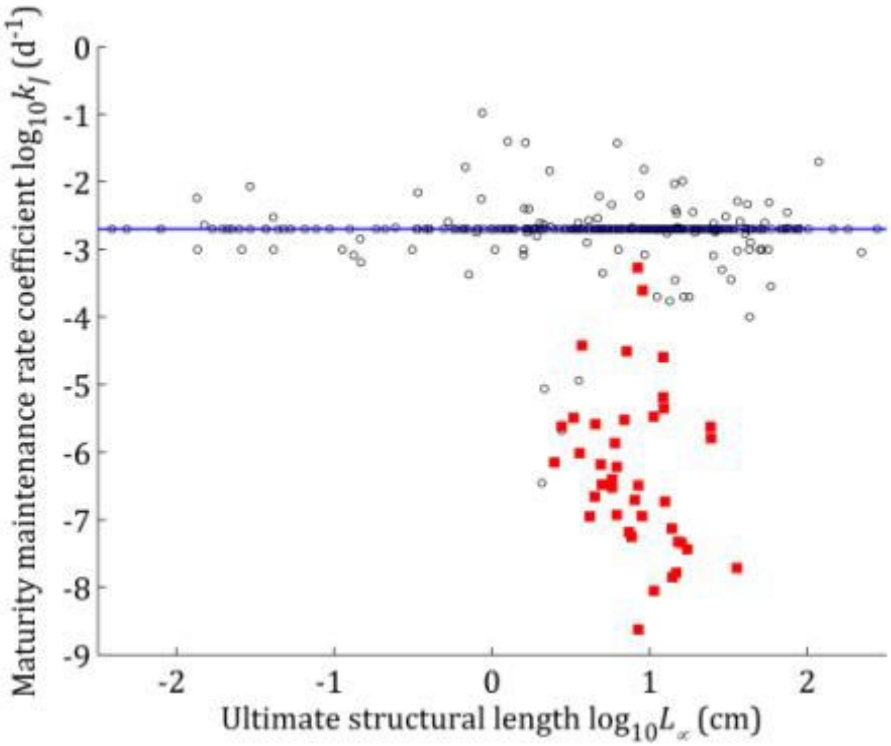

Figure 2.8 – Log-log plot of the maturity maintenance rate coefficient ($\dot{k}_J$, d^{-1}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. Marker codes: squares – bird species; circles – other organisms from the "Add_my_pet" library. The line represents the expected values according to the generalized animal.

2.3.3.9 Specific cost for structure ([E_G], J cm^{-3})

The specific cost for structure ([E_G], J cm^{-3}) is not expected to scale with body size and, as expected, it does not increase with increasing L_∞ for birds. The low scatter of values observed for this parameter reflects the similar low scatter of the wet weight / dry weight ratio values. The reason for this results from the use of a common κ_G of about 0.8 among the species (used as a pseudo-data during the parameterization process in the absence of real efficiency values) that constrains the variation in [E_G]. All the values are above the expectation from the generalized animal but this is due to the fact that for the generalized animal a specific density of d_V = 0.2 g cm^{-3} is assumed while for birds the average observed is close to 0.4 g cm^{-3} (Figure 2.9).

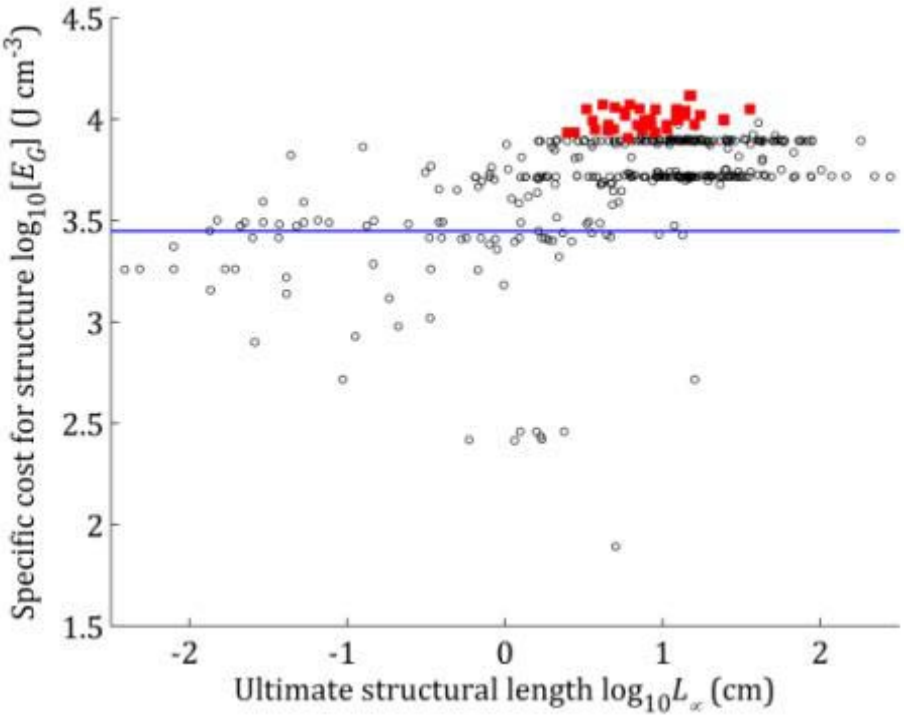

Figure 2.9 – Log-log plot of the specific cost for structure ([E_G], J cm^{-3}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. Marker codes: squares – bird species; circles – other organisms from the "Add_my_pet" library. The line represents the expected values according to the generalized animal, assuming a specific density of d_V = 0.1 g cm^{-3}.

2.3.3.10 Weibull ageing acceleration ($\ddot{h}_a$, d^{-2})

The Weibull ageing acceleration ($\ddot{h}_a$, d^{-2}) values estimated for birds stand out as being spread along a range that begins with a very low value for the Common Swift and ends with the value for the Greater Rhea – a value positioned close to the where most values estimated for other organisms are located. All the values are below the expectations from the generalized animal. This parameter is supposed to increase with increasing L_∞ and the values for the birds seem to follow this pattern. Notwithstanding, the other ageing parameter used in the standard DEB model – the Gompertz stress coefficient (s_G) (-) – used to estimate the expectations from the generalized animal is typically much closer to zero (1×10^{-4}) (corresponding to what is expected from an ectotherm, with the life span hardly depending on the maximum body size) than the value we used for the bird species (0.01) (Figure 2.10).

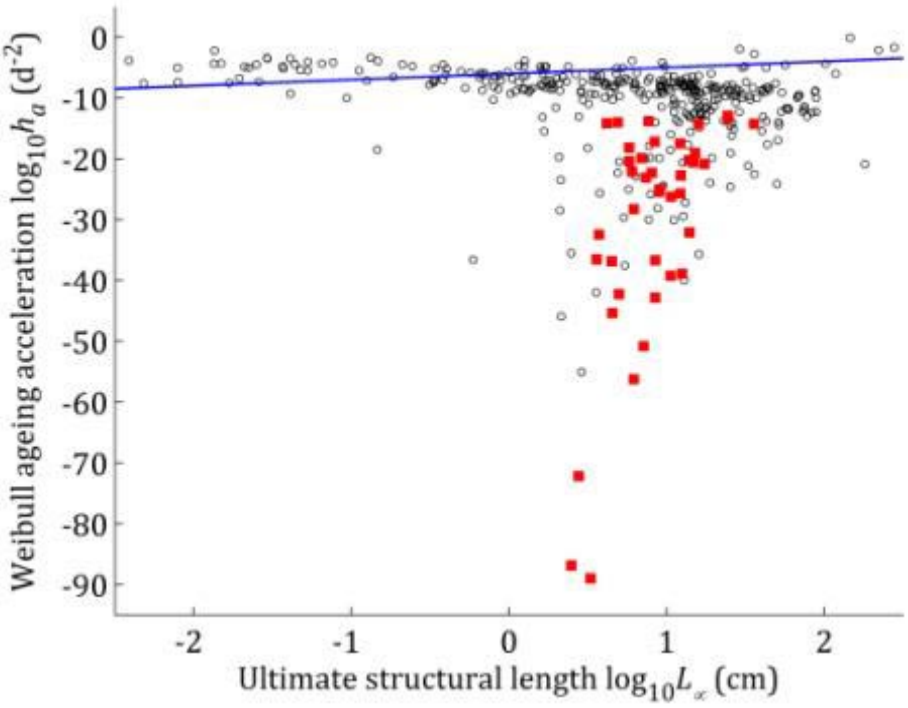

Figure 2.10 – Log-log plot of the Weibull ageing acceleration ($\ddot{h}_a$, d^{-2}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. Marker codes: squares – bird species; circles – other organisms from the "Add_my_pet" library. The line represents the expected values according to the generalized animal.

2.3.4 Secondary patterns

2.3.4.1 Somatic maintenance rate coefficient ($\dot{k}_M$, d^{-1})

The somatic maintenance rate coefficient ($\dot{k}_M$, d^{-1}) is expected to be independent of body size. However, the estimated values decline as L_∞ increases, driven by the previously observed pattern regarding [$\dot{p}_M$] and L_∞. The estimated values are positioned above and below the expectations from the generalized animal (Figure 2.11).

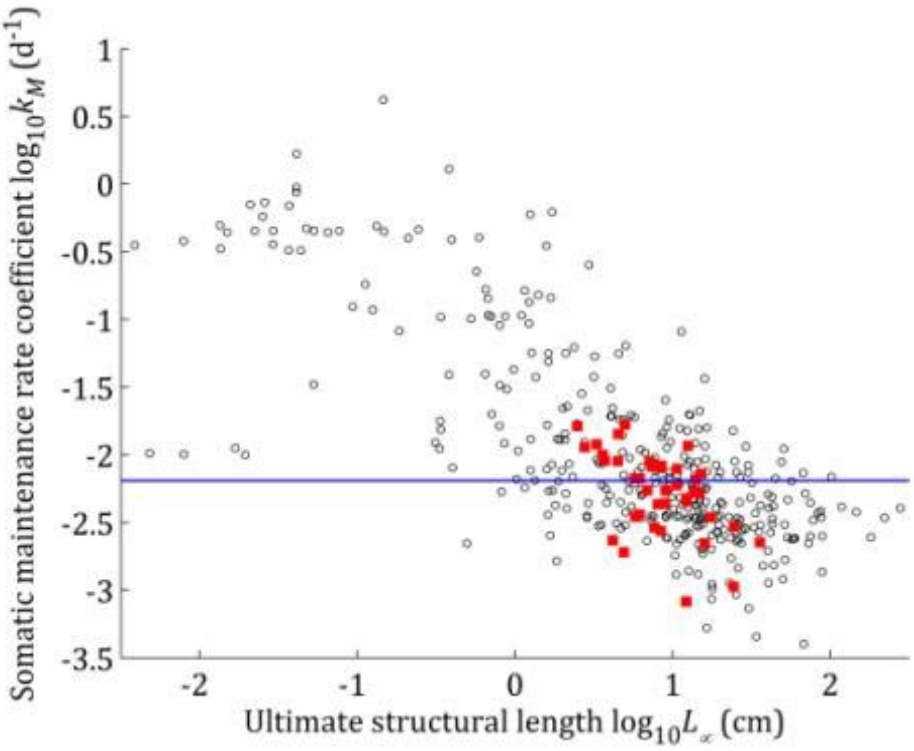

Figure 2.11 – Log-log plot of the somatic maintenance rate coefficient ($\dot{k}_M$, d^{-1}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. Marker codes: squares – bird species; circles – other organisms from the "Add_my_pet" library. The line represents the expected values according to the generalized animal.

2.3.4.2 Maximum reserve capacity ([E_m], J cm^{-3})

The maximum reserve capacity ([E_m], J cm^{-3}) is expected to increase with increasing L_∞, considering the expected increase in $\{\dot{p}_{Am}\}$ and considering that $\dot{v}$ is expected to be independent from body size. Our results fit with these expectations as $\{\dot{p}_{Am}\}$ increases and $\dot{v}$ actually decreases with L_∞. Most of the estimated values are below the expectations from the generalized animal, but the expected maximum reserve capacity of the Wandering Albatross lies within this range and three species have higher values than those expected: the Cuckoo Roller, the White-breasted Mesite and the Barn Owl. This is mostly due to the relatively low $\dot{v}$ values of these species. However, in the case of the Cuckoo Roller and the White-breasted Mesite, these may be underestimations as there were no growth data available to include (Figure 2.12).

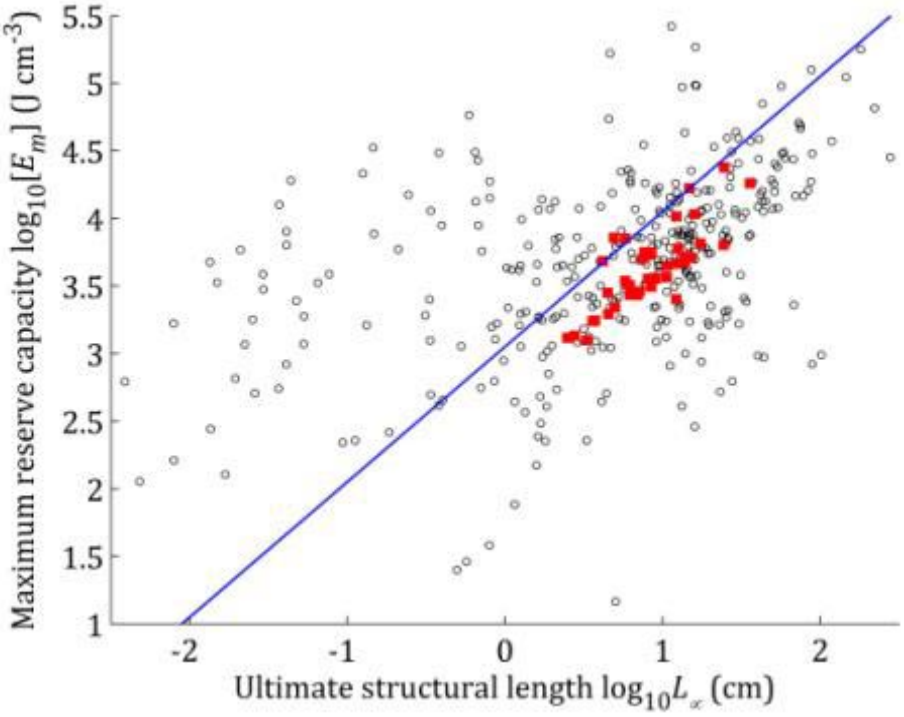

Figure 2.12 – Log-log plot of the maximum reserve capacity ([E_m], J cm^{-3}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. Marker codes: squares – bird species; circles – other organisms from the "Add_my_pet" library. The line represents the expected values according to the generalized animal.

2.3.4.3 von Bertalanffy growth rate ($\dot{r}_B$, d^{-1})

The estimated von Bertalanffy growth rate ($\dot{r}_B$, d^{-1}) values for birds are relatively high and above the expectations from the generalized animal. Below the expectations are the estimated growth rates of the Cuckoo Roller, the White-breasted Mesite, the North Island Brown Kiwi and the Greater Rhea. As it was mentioned before, the absence of post-hatching growth data for the first two species suggests that the estimated growth rates may be underestimated. The last two species are slow growing Palaeognathae. This parameter is expected to decrease with increasing L_∞ and our results confirm this trend. The declining $\dot{k}_M$ as L_∞ increases greatly contributes to this result (Figure 2.13).

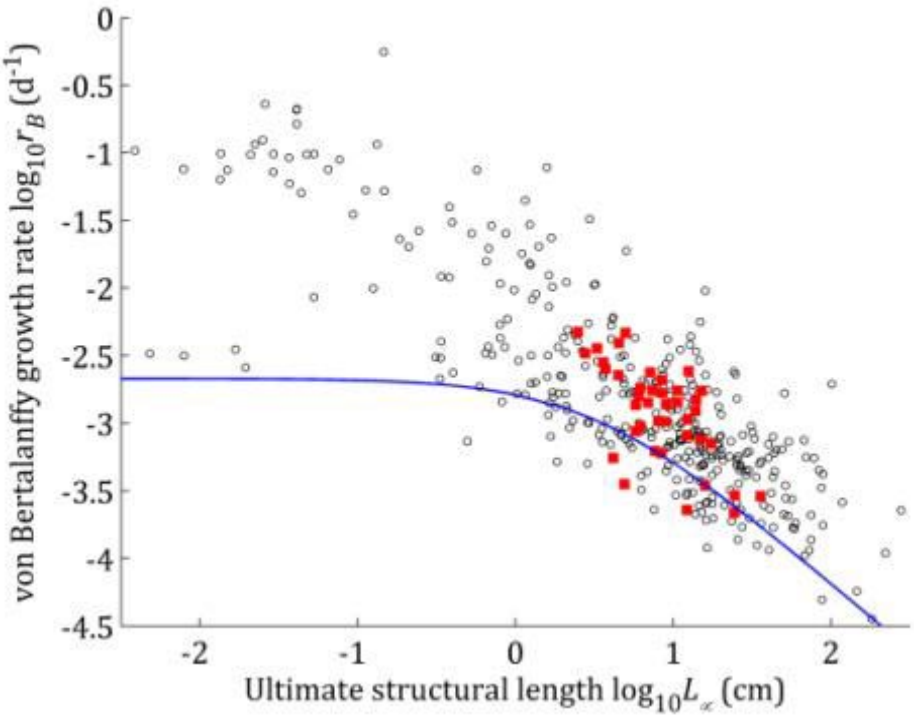

Figure 2.13 – Log-log plot of the von Bertalanffy growth rate ($\dot{r}^T_B$, d^{-1}) as a function of the ultimate structural length (L_∞, cm) at each specific average adult body temperature. Marker codes: squares – bird species; circles – other organisms from the "Add_my_pet" library. The line represents the expected values according to the generalized animal.

2.3.4.4 Dry mass-specific respiration (-J_O / W_d, L g-1 h-1)

There is no assumption underlying the estimation of respiration values in DEB theory. The fluxes are estimated based on the conservation of chemical elements (C, H, O and N) and therefore every energy flux (assimilation, somatic and maturity maintenance and reproduction overheads) has an effect on these values. Given that [E_m] is expected to increase with increasing L_∞ (and with birds that is exactly the case, as we have seen), we may expect mass-specific respiration to decline as body size increases. Recently Kooijman and Lika (2014a) observed that in fish the dry mass-specific respiration approximately decreases with the maximum dry weight to the power ¼. Such decrease had already been suggested (Maino et al., 2014) (Table 2.7). According to our results, the dry mass-specific respiration (-J_O / W_d, L g^{-1} h^{-1}) follows the expected pattern, decreasing with increasing L_∞. Most of the values exhibited by the sampled bird species are aligned with the expectations computed for the generalized animal. The species exhibiting the lowest values included the two species that were included without post-hatching data – the Cuckoo Roller and the White-breasted Mesite – and three slow growing Palaeognathae – the North Island Brown Kiwi, the Greater Rhea and the Emu (Figure 2.14).

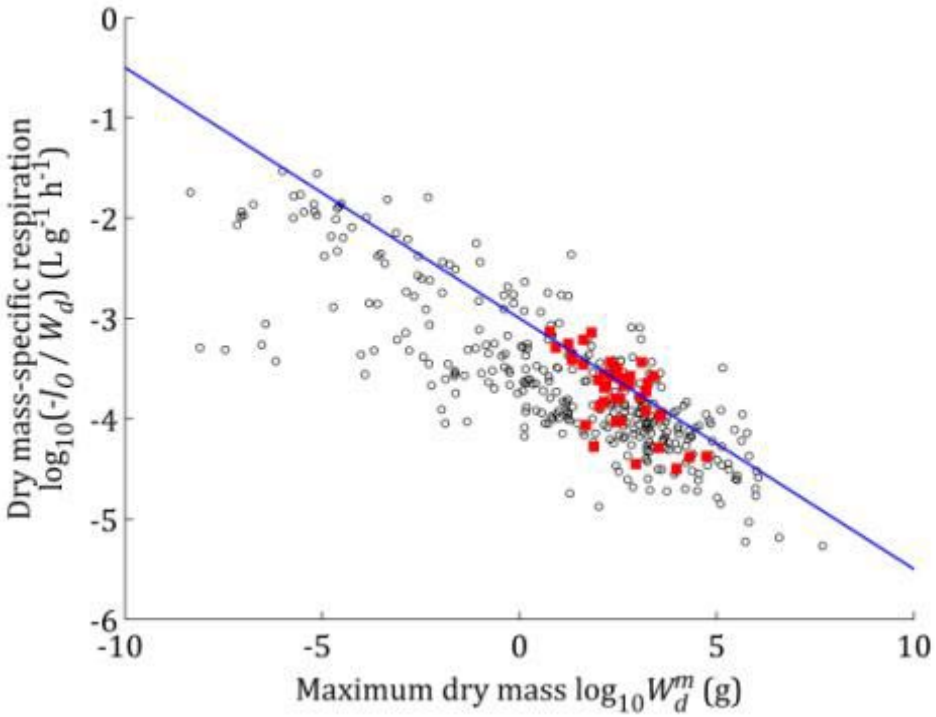

Figure 2.14 – Log-log plot of the dry mass-specific respiration (-J_O / W_d, L g^{-1} h^{-1}) as a function of the maximum dry mass (W_d^m, g) at the reference temperature of 293 K. Marker codes: squares – bird species; circles – other organisms from the "Add_my_pet" library. The line represents the expected values according to the generalized animal.

2.3.4.5 Fasting capacity (t_s, d)

The fasting capacities (t_s, d) of birds seem to be among the lowest estimated when we compared birds with other organisms. The fasting capacity is expected to scale with L_∞ due to the corresponding relationship between $[E_m]$ and L_∞ and the expected independent nature of $[\dot{p}_M]$. The values for our sampled bird species increase with increasing L_∞, as expected due to the increase in $[E_m]$, but the slope of this trend seems to be steeper due to the strong negative correlation we observed between $[\dot{p}_M]$ and L_∞. For larger birds, which are mostly flightless or almost flightless, the steeper decrease in somatic maintenance costs coupled with higher reserve capacities due to their size, provides higher fasting capacities and lower starvation risks (Figure 2.15).

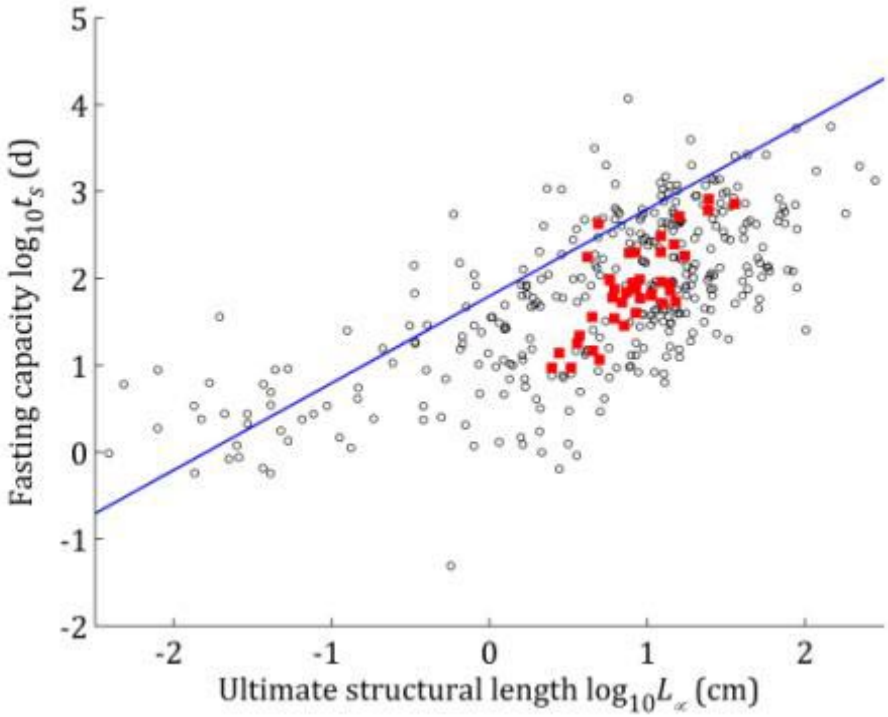

Figure 2.15 – Log-log plot of the fasting capacity (t_s, d) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. Marker codes: squares – bird species; circles – other organisms from the "Add_my_pet" library. The line represents the expected values according to the generalized animal.

2.3.4.6 Maximum wet weight per ultimate structural volume (W_w^m / L_∞^3, g cm^{-3})

The maximum wet weight per ultimate structural volume (W_w^m / L_∞^3, g cm^{-3}) is expected to scale with L_∞ due to the contribution of the reserve capacity to weight ([E_m] scales with L_∞). The computed values for the birds increase with increasing L_∞ but not as steeply as expected from the generalized animal. The estimated values for bird species are among the lowest, for endotherms, suggesting that this trait may have co-evolved with the capacity to fly (Figure 2.16).

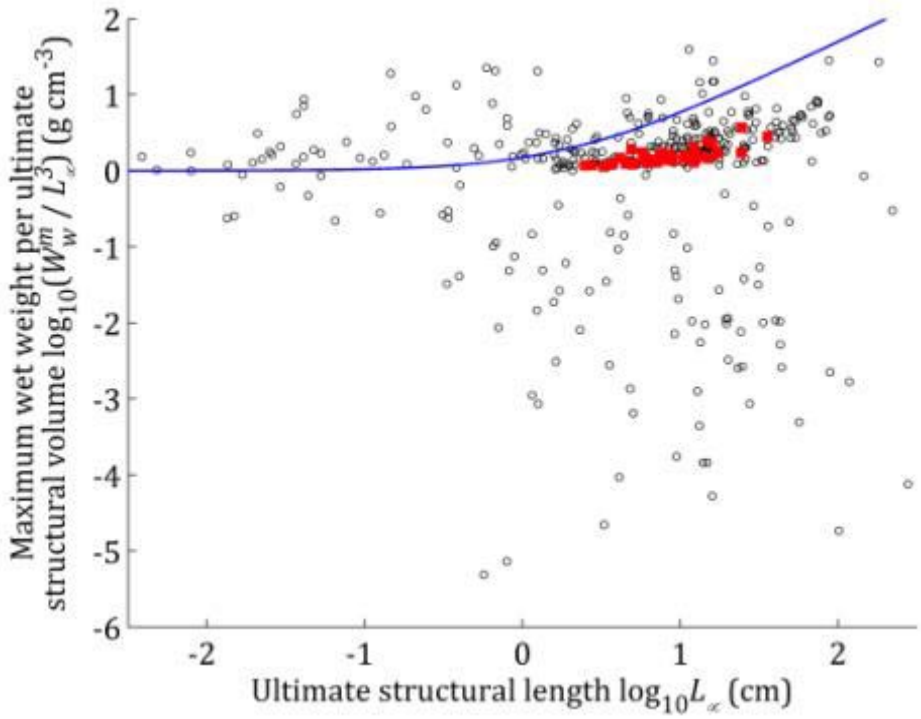

Figure 2.16 – Log-log plot of the maximum wet weight per ultimate structural volume (W_w^m / L_∞^3, g cm^{-3}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. Marker codes: squares – bird species; circles – other organisms from the "Add_my_pet" library. The line represents the expected values according to the generalized animal.

2.3.4.7 Initial egg mass (M_E^0, C-mol)

The initial egg mass (M_E^0, C-mol) is expected to increase with L_∞^4 due to the fact that $[E_m]$ increases with L_∞ and the structural volume of the hatchling increases with L_∞^3. Our DEB estimates for bird species are aligned with these expectations. The distribution of these values exhibits the lowest amount of scatter and most of the values for the birds are aligned with the expectation from the generalized animal. However, some of the smaller bird species have slightly larger eggs than expected and some of the larger ones have smaller eggs than expected (Figure 2.17).

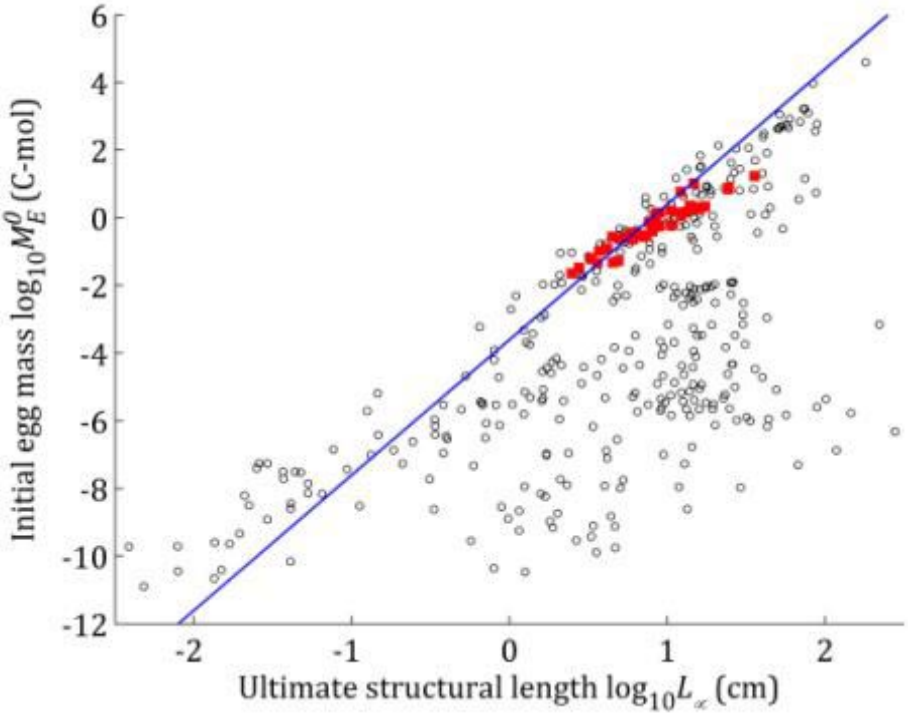

Figure 2.17 – Log-log plot of the initial egg mass (M_E^0, C-mol) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. Marker codes: squares – bird species; circles – other organisms from the "Add_my_pet" library. The line represents the expected values according to the generalized animal.

2.3.4.8 Specific allocation to reproduction per maximum structural volume ($\dot{p}_R^m / L_m^3$, J d^{-1} cm^{-3})

The estimated values for the specific allocation to reproduction per maximum structural volume ($\dot{p}_R^m / L_m^3$, J d^{-1} cm^{-3}) are lower than the expectations from the generalized animal and are among the lowest considering the whole library of parameterized organisms. This is not surprising considering the typical high post-hatching growth rates of birds. The allocation to reproduction is expected to increase with L_m^3 and the volume-specific value is therefore expected to be constant. However, there seems to be a slight negative correlation with L_∞ for birds. The constraint this pattern constitutes for bird species may have considerable evolutionary relevance. Selective pressures towards an increase in reproductive effort may drive a trend of body size decrease (Figure 2.18).

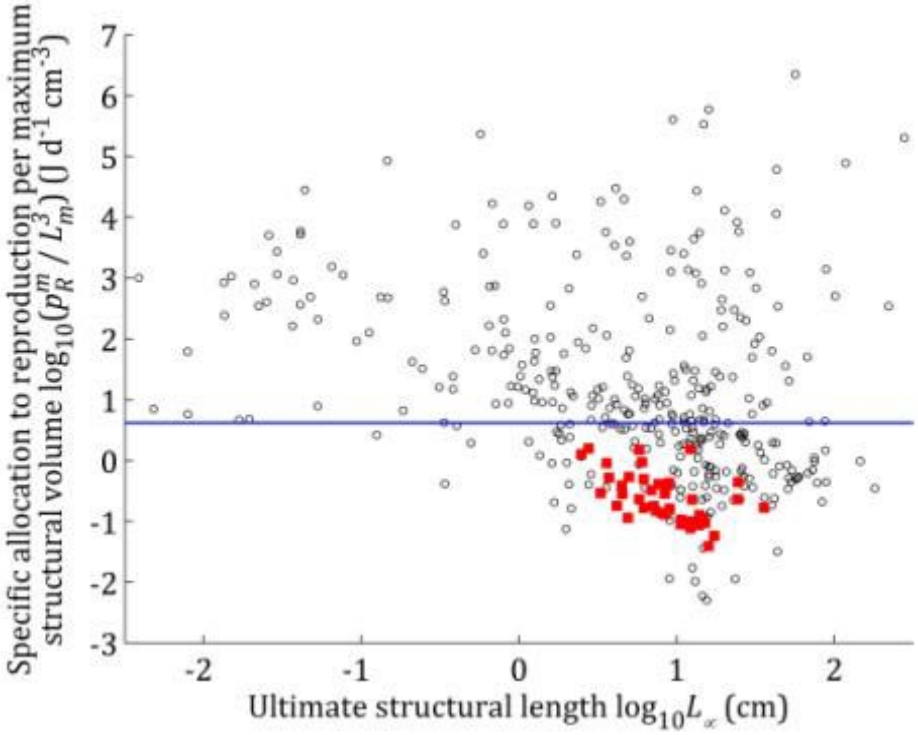

Figure 2.18 – Log-log plot of the specific allocation to reproduction per maximum structural volume ($\dot{p}_R^m / L_m^3$, J d^{-1} cm^{-3}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. Marker codes: squares – bird species; circles – other organisms from the "Add_my_pet" library. The line represents the expected values according to the generalized animal.

2.3.4.9 Maturity maintenance at puberty per maximum structural volume ($\dot{p}_J^p / L_m^3$, J d^{-1} cm^{-3})

The maturity maintenance at puberty per maximum structural volume ($\dot{p}_J^p / L_m^3$, J d^{-1} cm^{-3}) is not supposed to scale with body size. However, there seems to be a slight decline, despite the scatter, as L_∞ increases in birds. However, this is mostly due to the slight decline previously observed regarding $\dot{k}_J$. Most the values are below the expectations from the generalized animal and among the lowest values obtained considering the whole collection of analysed organisms, a result which is consistent with the typically high post-hatching growth rates of birds and low maturity maintenance rate values. Three species exhibit values above those expected from the generalized animal: the Kagu, the Red Junglefowl and the North Island Brown Kiwi. The first two stand out as having the two highest $\dot{k}_J$ values among our sample and the Kiwi for having one of the highest investments of energy in maturity up to the puberty threshold (E_H^p) and a reasonably high $\dot{k}_J$ (Figure 2.19).

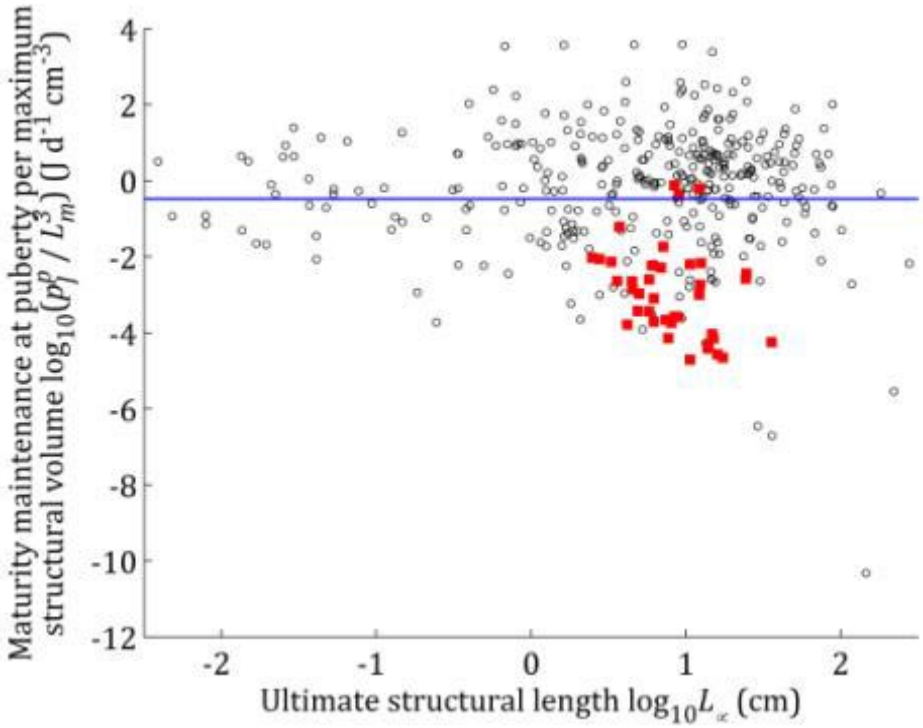

Figure 2.19 – Log-log plot of the maturity maintenance at puberty per maximum structural volume ($\dot{p}_J^p / L_m^3$, J d^{-1} cm^{-3}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. Marker codes: squares – bird species; circles – other organisms from the "Add_my_pet" library. The line represents the expected values according to the generalized animal.

2.4 Discussion

2.4.1 Parameterization

The covariation method provided estimates for the core DEB parameters that allowed for consistently high FIT values either using a constant maturity density ($\dot{k}_J = \dot{k}_M$) or allowing for the maintenance rates to differ ($\dot{k}_J \neq \dot{k}_M$). However, the second approach provided a significantly better FIT value and allowed for better adjustments between the observed and DEB estimated growth curves particularly in the case of bird species that reach specific maturity thresholds much before or after the somatic growth seems to be complete (e.g., the Red Junglefowl and the Wandering Albatross, respectively), i.e., the metabolic switches related to maturity do not seem to occur at fixed amounts of structure. Previous studies advised for this approach to be used when growth data obtained at different food levels, is available (Kooijman et al., 2008; Sousa et al., 2010). Our results suggest that even in the absence of such growth data, allowing for the maintenance rates to be estimated independently may fit better with the species we are working with but further studies focusing on different taxa may be helpful to evaluate this suggestion, particularly if growth data at different food levels is available and results can be compared.

The high FIT values obtained indicate which means that these sets of parameters it was possible to estimate values for both the zerovariate and univariate life history traits with great precision when compared to the observed values. The von Bertalanffy growth curves provided good fits to the observed growth curves for most species (e.g., the Kagu and the North Island Brown Kiwi) but for some species the adjustment was not so precise (e.g., the Great Northern Loon and the Micronesian Kingfisher). The growth pattern of the Great Northern Loon exemplifies a typical avian deviation from the von Bertalanffy growth pattern towards the logistic growth pattern. This growth pattern occurs even when food resources are abundant and may result from a thermal ontogeny that includes the transition from a state with almost no thermoregulation (which may last up to a few days after hatching, particularly in altricial species) to a state with full thermoregulatory capacity. During this transitional period the insulation and/or heat transfer from the progenitor(s) to the hatchling changes and body temperature variation will affect metabolic rates and consequently the growth rate (Konarzewski et al., 1998; Kooijman, 2010a; Zonneveld and Kooijman, 1993). The growth pattern of the Micronesian Kingfisher also deviates from the von Bertalanffy growth pattern but for a different reason. This species exhibits a consistent increase in body weight up to values that are higher than the observed average adult body weight, followed by a gradual decrease down to the adult values. This pattern is observed in species belonging to groups such as the Falconiformes, Apodiformes, Suliformes and Procellariiformes, and may be driven by a decline in food availability before fledging, coupled with differences in locomotion effort and somatic maintenance costs between the nestling and fledgling stages, as it has been demonstrated for the Wandering Albatross (Teixeira et al., 2014).

However, considering the large distribution of values observed for several of the data used as input information (Table 2.3), the differences between each species are hardly affected by a less accurate adjustment of the von Bertalanffy growth curve to the data points.

Regarding the zerovariate data, precise estimates for most life history traits can be obtained using the estimated DEB parameters' values, except for the cases of a_h and a_p. The best overall DEB parameter sets produced underestimations regarding the duration of the incubation period and the onset of sexual maturity, for some species (Table 2.12).

In the case of the incubation period several reasons may help explaining the residuals we observed. For the parameterization procedure an average incubation temperature was taken into account, however during incubation the eggs are usually subjected to gradients of temperature variation (Deeming and Ferguson, 1991b) and in some cases (e.g., pelagic feeders) periods without the presence of any progenitor during which a considerable cooling of several degrees takes place prolonging the incubation period. This increase seems to result from decreases in the growth rate. In the case of the Fork-tailed Storm-petrel (*Oceanodroma furcata*), for instance, an average incubation temperature of 37 °C (in an incubator) reduces the incubation length to half the duration observed in natural conditions with an average incubation temperature of 34 °C (Vleck and Kenagy, 1980). The periods of increase in temperature, which happen occasionally during incubation and during the post-hatching thermal ontogeny, as referred before, accelerate metabolic rates – a kind of acceleration that has recently been designated as Type-T acceleration (Kooijman, 2014b) – and affect the growth pattern.

The occurrence of diapauses is another possible explanation (Kooijman, 2010a). The time it takes for the embryo to develop may actually be shorter than the observed incubation period. However, for some of the species considered in our sample the set of DEB parameters estimated under the average temperature conditions used (with an average egg temperature value for the incubation period and a distinct, specific, average body temperature value for the post-hatching stages) provided accurate estimates for both the embryonic and post-hatching stages. This was mostly the case for the five species belonging to Palaeognathae. All the species belonging to this Superorder are accurately modelled except for the Emu which has an underestimated incubation period (about 38 d compared to the observed 53 d). Notwithstanding the differences are significant between the Neognathae and the Palaeognathae regarding the residuals for both the incubation duration (U (38) = 13, n_1 =35 n_2 = 5, p = 2.44 × 10^{-3}) and the onset of sexual maturity (U (38) = 20, n_1 =35 n_2 = 5, p = 6.14 × 10^{-3}) (Table 2.12). One possible evolutionary explanation for these differences emerges from selective pressures related to environmental factors such as predation, driving the acceleration of post-hatching growth rates in many smaller Neognathae species. The Palaeognathae, taking advantage of their large size or of an absence of mammalian predators throughout their evolution, such as in the case of the ancestral Kiwi species, may have not been selected positively as far as a quicker post-hatching growth rate is concerned. At least for the several extant Kiwi species, the situation has changed and predatory pressure, mostly from introduced mammals, is now one of the causes for serious population decline (Sales, 2005). In any case, the evolution of growth rates may have also been physiologically constrained as we will discuss further ahead.

Concerning sexual maturity, how much of the residuals result from error is uncertain considering that for most species the exact onset of sexual maturity is unknown and the age at first reproduction may actually take place much later due to environmental (e.g., seasonality) and behavioural reasons. In fact, it has already been pointed out that in species such as the Budgerigar (*Melopsittacus undulatus*), where reproduction in captivity has been observed to occur before the usual age at first reproduction in the wild, metabolism may actually be down-regulated throughout the non-breeding season (Kooijman and Lika, 2014b).

Table 2.12 – Statistical details regarding the residuals from: a) a_h – the incubation period duration (d); and b) a_p – sexual maturity (d), and according to the Superorder. Statistical abbreviations are as follow: $\bar{x}$ – mean; SE – standard error; $\tilde{x}$ – median; Q_1 – lower quartile; Q_3 – upper quartile; c_v – coefficient of variation.

Superorder		a_h (d)	a_p (d)
Neognathae	$\bar{x}$	21	406
	SE	2	77
	$\tilde{x}$	20	243
	Q_1	14	0
	Q_3	27	590
	c_v	0.5	1.2
Palaeognathae	$\bar{x}$	3	0
	SE	1	0
	$\tilde{x}$	0	0
	Q_1	0	0
	Q_3	0	0
	c_v	2.2	2.0

2.4.2 DEB parameters

The diversity of values estimated for the set of DEB parameters presented in Table 2.9, Table 2.10 and Table 2.11 generally reflect the diversity of life history traits observed in birds. E_H^b is the parameter with the highest degree of variation despite the fact that a_h has a coefficient of variation ten times lower. The cumulated energy invested in maturation up to fledging and puberty (E_H^x and E_H^p, respectively) also exhibit high variation coefficients. Considering that these parameters scale with the ultimate (adult) structural length of species, then this variation in the cumulated energy invested in maturation is expected to occur in samples with a large range of body length values such as the one used in this study. This variation, particularly regarding the incubation period and up to fledging, seems to conflict with the strong phylogenetic inertia that Pienaar *et al.* (2013) observed affecting the incubation and fledging times. This illustrates the relevance of addressing the differences in embrionary development from an energetic point of view, taking into consideration not just the duration of that stage, or the egg size, but the amount of energy invested in somatic growth and maturity. The variation we observe in the estimated cumulated energy invested in maturation during the embryonic stage suggests that if further studies on phylogenetic inertia take these values into consideration, the estimated inertia associated with the incubation period will probably be lower.

Overall, the parameter with the lowest amount of variation was κ, suggesting that the allocation of energy to somatic growth and maintenance or to maturation, maturity maintenance and reproduction, may have been subject to the highest degree of phylogenetic inertia throughout the evolution of birds. Considering that the average κ was very high (0.988), it seems that selective pressures have mostly driven birds towards larger investments in growth (i.e., an evolutionary down-regulation of reproduction), which challenges the traditional interpretation of the role of reproduction and reproduction costs in the overall fitness and adaptive capacity of a species and particularly in the life history study of birds (King, 1973; Lindén and Møller, 1989; Sibly et al., 2012; Wiersma et al., 2004). However, a small change in κ may have a considerable and visible impact in both growth and reproduction and all the associated life history traits. The very high average observed for κ associated to very low values for $\dot{k}_J$ may also express the general trend in birds to start reproducing after their body weight has reached an asymptote, i.e., they may incorporate some error associated with two facts: a) for most species we do not know exactly when sexual maturity has been

reached, and b) we may be averaging the fluctuating effects of seasonality throughout the life cycle of birds. The high κ values observed also suggests that most bird species seem to adjust to the recently proposed waste-to-hurry hypothesis, according to which species evolve high maintenance costs in order to grow fast, remain small and respond quickly to temporal and local food abundance (Kooijman, 2013). One interesting example regarding this hypothesis concerns the Iceland's sea ducks. Known for spending part of the year at sea, they gather in groups just before the breeding season and perform inland excursions to assess the seasonal progress and fine-tune the onset of their breeding season. These birds actually start breeding on snow-covered land and have a breeding window of less than two weeks.

It seems that despite the low variation in κ, the diversity of values observed for other parameters, particularly those related to maturity, may be enough to provide the diversity we observe today regarding the ages at which birds hatch, fledge, and reach puberty or senesce. Also according to our results, the variation in the rates of mobilisation of energy from reserves or somatic maintenance may play a moderate role in the evolution of birds. Recently McNab (2012) criticized Lovegrove (2009) regarding his observation according to which currently living species are facing the challenge of adaptation to contemporary global changes in a context of phylogenetic inertia. McNab (2012) criticizes the idea of phylogenetic inertia and the constraint it represents but our results suggest that, metabolically speaking, different degrees of inertia depending on the metabolic process may constraint adaptation. Currently living species will probably not be able to adapt quickly by allocating a larger fraction of energy to reproduction in detriment of somatic growth and maintenance (i.e., changing κ) due to the apparent phylogenetic stability and low variation of this parameter, but may be able to adapt through the apparently higher plasticity in maturity-related and reserve mobilisation traits. Land-use change (Pereira et al., 2004) and climate change (Langham et al., 2014) are constraining ecological niches. Selective pressures may favour genotypes that allow strategies which are adjusted to the new bioclimatic contexts, such as higher growth rates that allow growth to be completed during shorter breeding seasons, even if at the cost of maturity (e.g., evolution towards altriciality) or higher assimilation and reserve mobilisation rates that co-evolve with quicker growth but also allow to take better advantage from shorter and irregular periods of abundance. The trade-offs may certainly express themselves through changes in body weight or length as well as through changes in reproductive output, survival rates and population dynamics. Through the application of DEB theory we may be able to understand how some of these trade-offs already take place by observing the patterns that emerge from the parameter sets, but further studies may also consider different scenarios of environmental change and model the effect those changes will have on the life histories of birds, as they are mediated through their metabolism.

2.5 Conclusions

By comparing the values of the primary and compound DEB parameters estimated for our sample of bird species with the corresponding values previously estimated for other organisms, it was possible to observe that bird species seem to exhibit extreme values regarding some these parameters and properties. For instance, birds display relatively high values of primary DEB parameters such as the allocation fraction to soma and the specific costs of structure, and of DEB properties such as the von Bertalanffy growth rate, the dry mass-specific respiration, the initial egg mass and the specific allocation to reproduction and maturity maintenance at puberty per maximum structural volume. On the other hand, birds also display relatively low values of primary DEB parameters such as the maturity maintenance rate coefficient and the Weibull ageing acceleration and of DEB properties such as the fasting capacity and the maximum wet weight per ultimate structural volume.

The estimated values for the DEB parameters of birds generally fit the expectations regarding the physical meaning of these parameters and their expected relationship with body size. However there are a few interesting exceptions. The distribution of the values estimated for some primary and compound DEB parameters that are intensive and not expected to scale with body size, exhibited a pattern that suggested such a relationship to occur, namely: the allocation fraction to soma, the energy conductance, the volume-specific somatic maintenance rate, the maturity maintenance coefficient, the somatic maintenance rate, the specific allocation to reproduction per maximum structural volume and the maturity maintenance at puberty also per maximum structural volume. The fact that these parameters and properties seem to scale with body size, even though it seems to be just a slight effect in some cases, may be of evolutionary relevance. Although the effect is not expected, there may have been selective pressures simultaneously driving changes in some metabolic traits and body size. For instance, the ability to fly may require smaller sizes but at the same time it may result in higher locomotion costs and require higher somatic maintenance rates.

All of the design DEB parameters and properties, that are expected to scale with body size, exhibited patterns that are consistent with these expectations. However, some of these, along with some of the parameters that are independent from body size, displayed distributions with considerable scatter. The way these values are scattered determines the diversity we currently observe in the life history traits of bird species. Much of this scatter may result from interactions and constraints that emerge from other metabolic processes. However, much of the scatter may also be associated with ecological factors such as the habitat, the diet, the ability to fly or to migrate, etc. Further studies researching these associations may help us to understand how the metabolism, the physiology, the ecology and the behaviour of bird species may have co-evolved throughout the evolution of birds.

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2.7 Appendix I

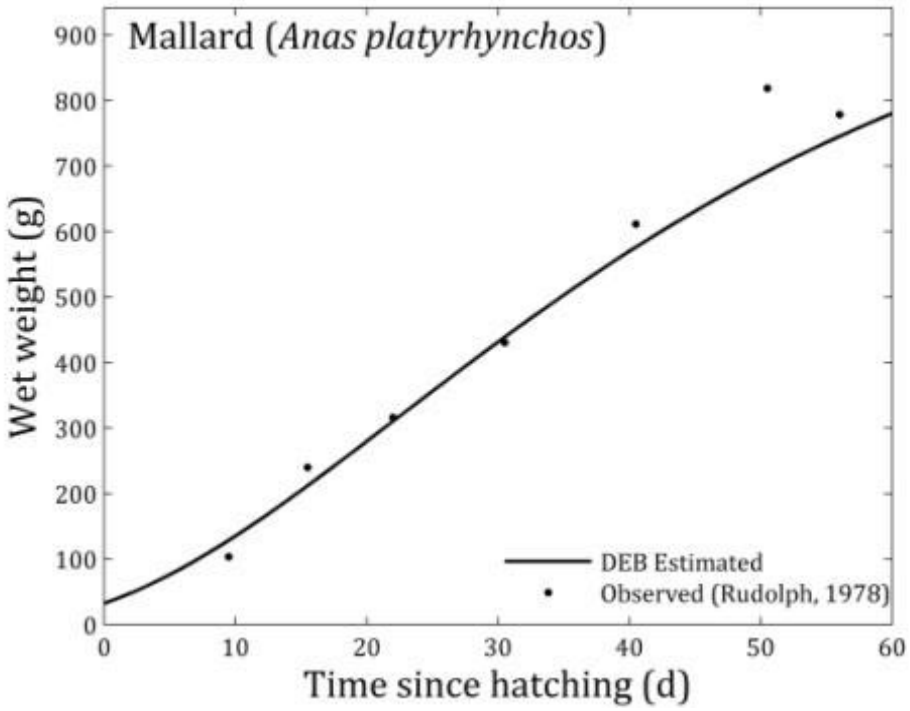

Figure 2.20 – Observed and DEB estimated wet weight growth curve for the Mallard (*Anas platyrhynchos*).

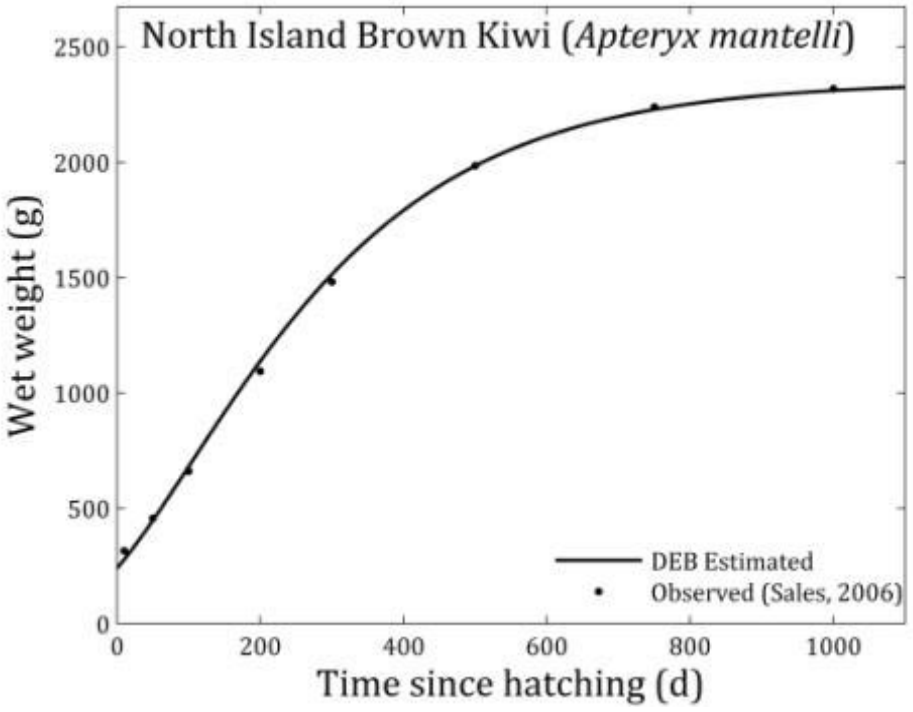

Figure 2.21 – Observed and DEB estimated wet weight growth curve for the North Island Brown Kiwi (*Apteryx mantelli*).

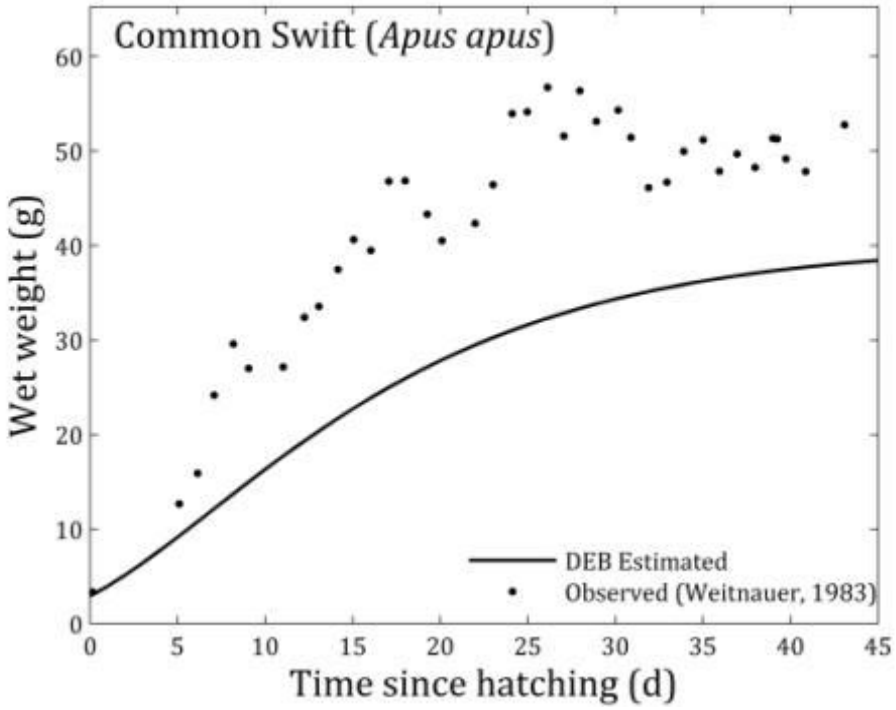

Figure 2.22 – Observed and DEB estimated wet weight growth curve for the Common Swift (*Apus apus*).

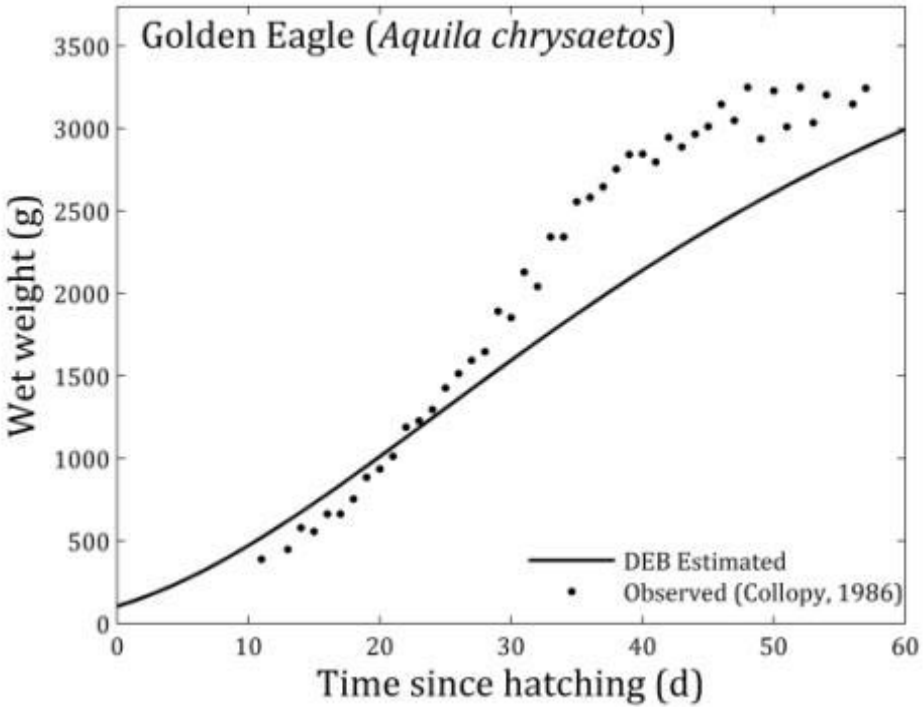

Figure 2.23 – Observed and DEB estimated wet weight growth curve for the Golden Eagle (*Aquila chrysaetos*).

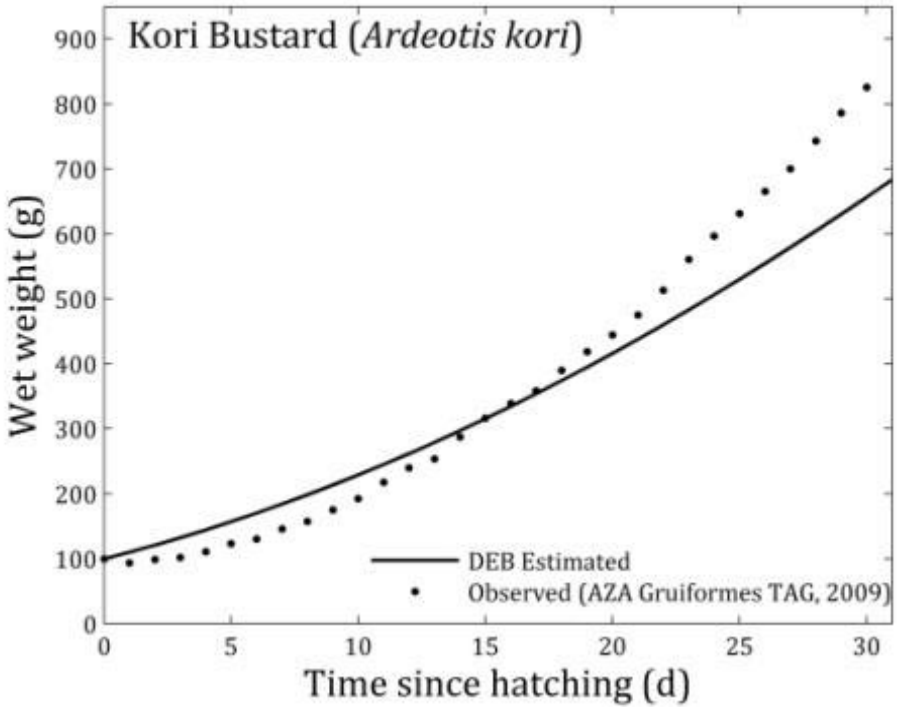

Figure 2.24 – Observed and DEB estimated wet weight growth curve for the Kori Bustard (*Ardeotis kori*).

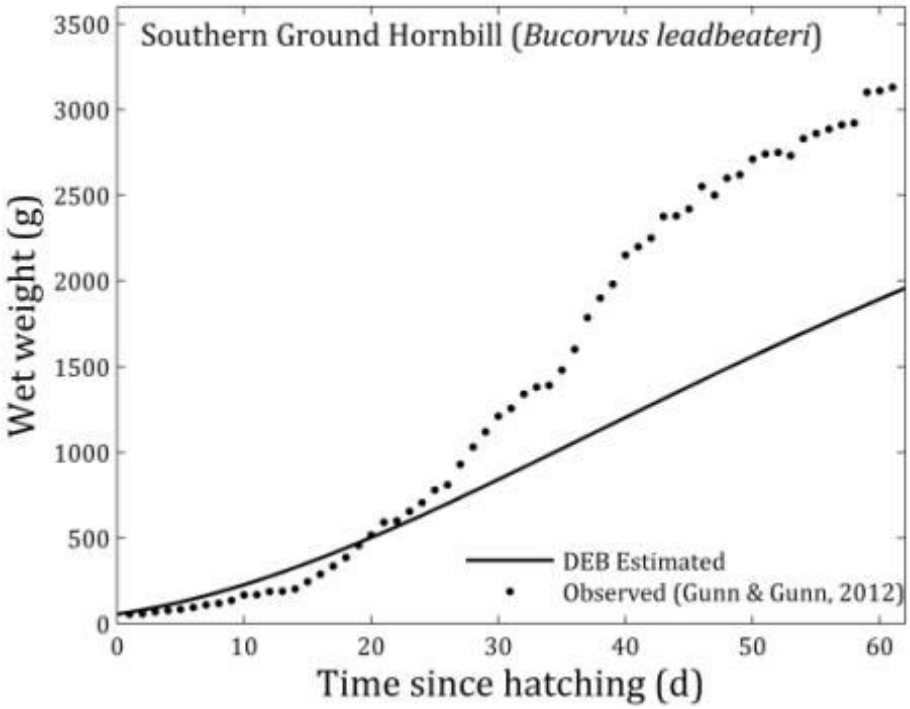

Figure 2.25 – Observed and DEB estimated wet weight growth curve for the Southern Ground Hornbill (*Bucorvus leadbeateri*).

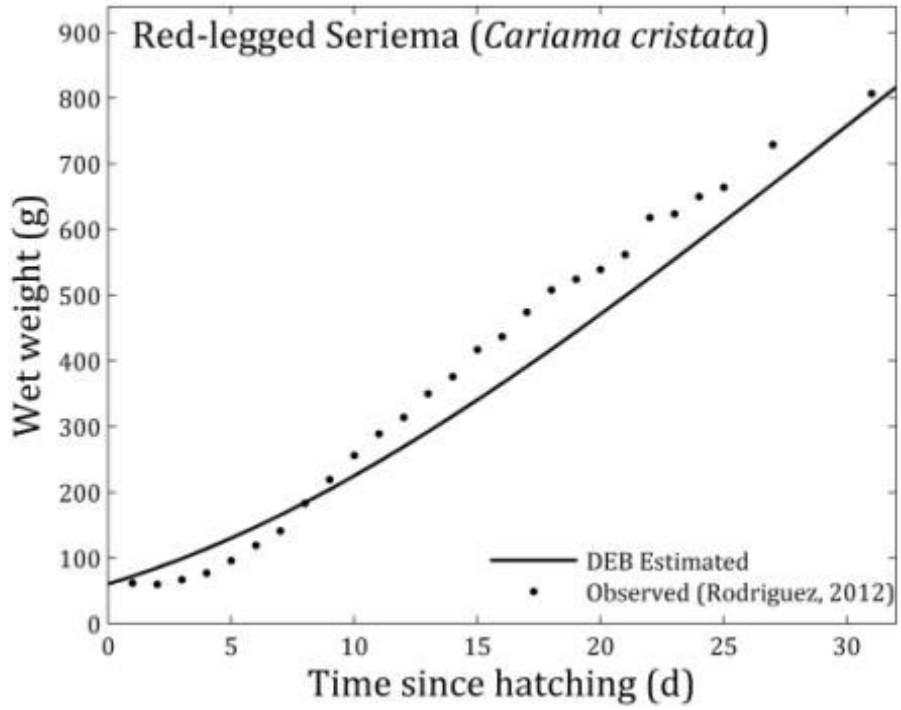

Figure 2.26 – Observed and DEB estimated wet weight growth curve for the Red-legged Seriema (*Cariama cristata*).

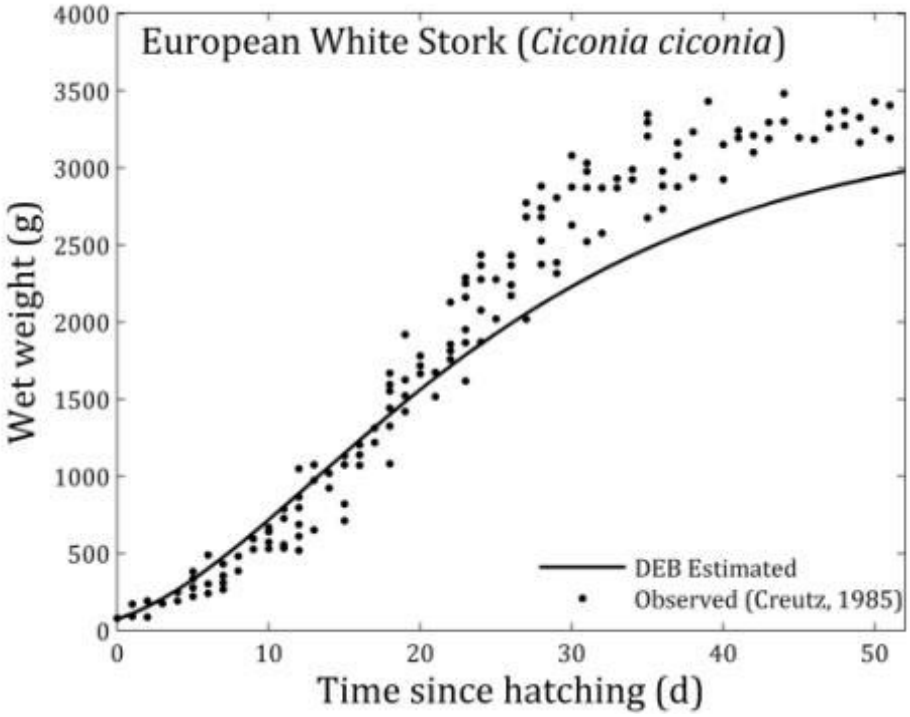

Figure 2.27 – Observed and DEB estimated wet weight growth curve for the European White Stork (*Ciconia ciconia*).

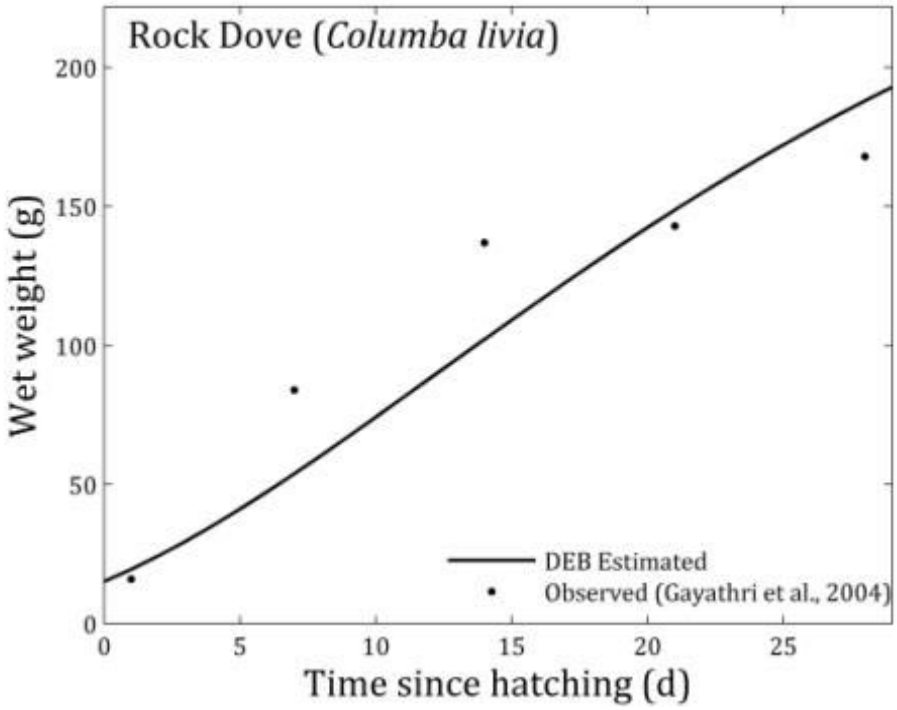

Figure 2.28 – Observed and DEB estimated wet weight growth curve for the Rock Dove (*Columba livia*).

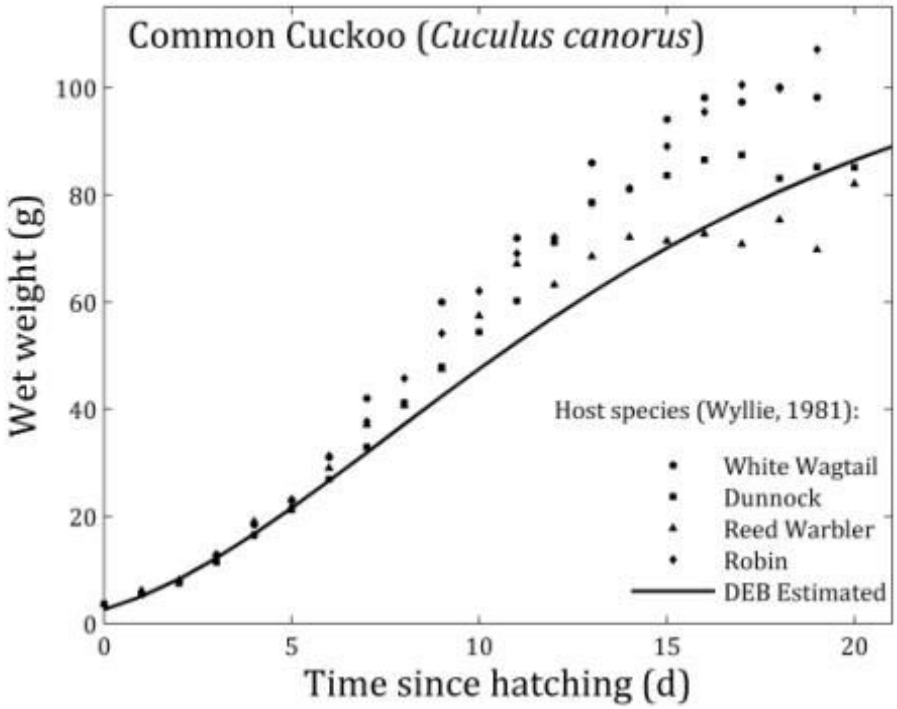

Figure 2.29 – Observed and DEB estimated wet weight growth curve for the Common Cuckoo (*Cuculus canorus*).

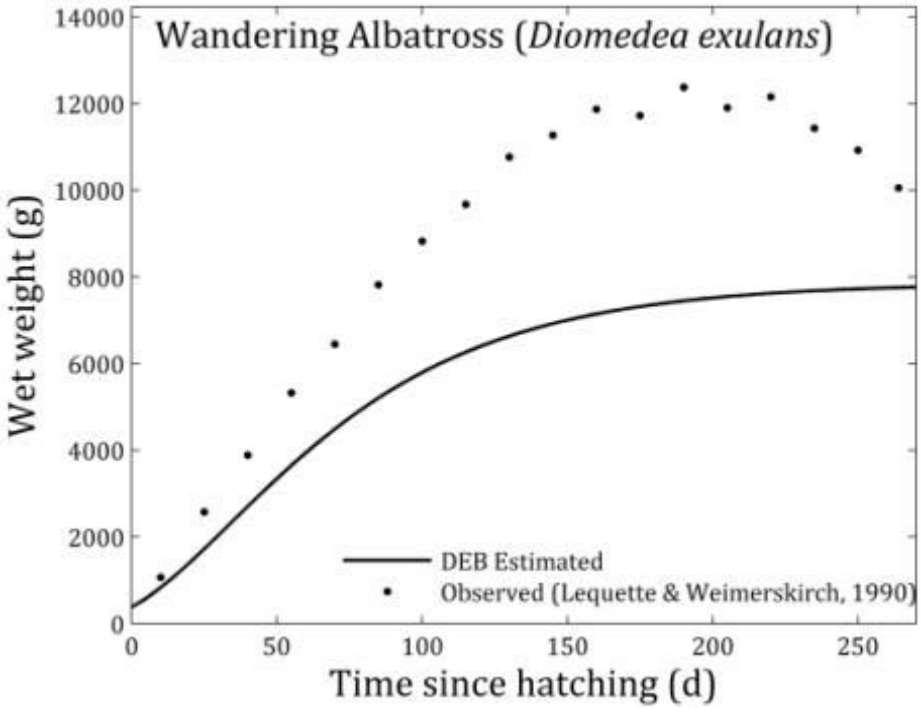

Figure 2.30 – Observed and DEB estimated wet weight growth curve for the Wandering Albatross (*Diomedea exulans*).

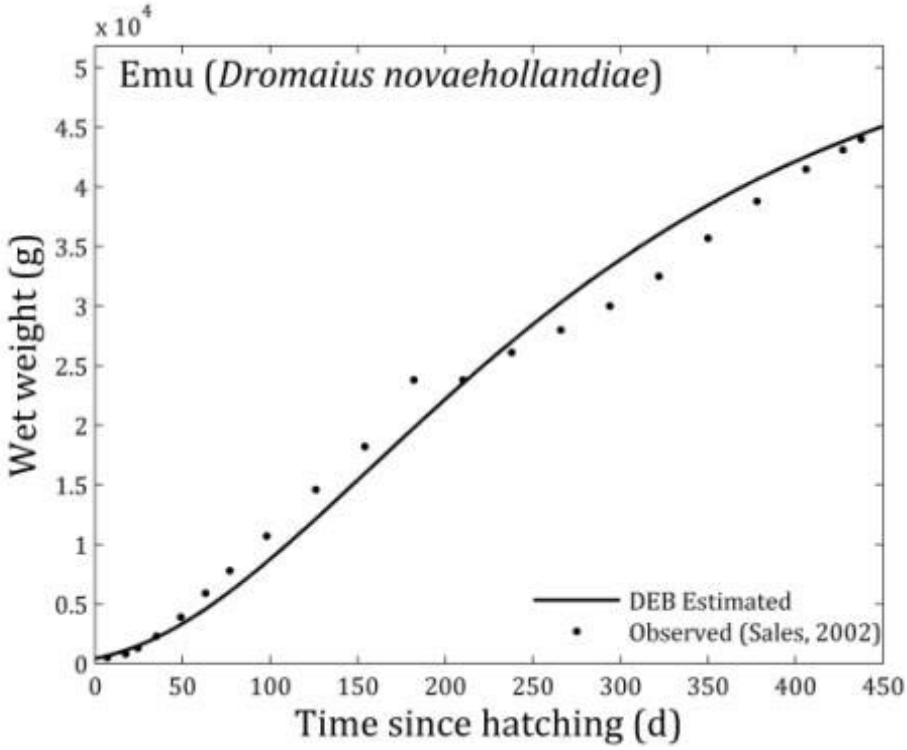

Figure 2.31 – Observed and DEB estimated wet weight growth curve for the Emu (*Dromaius novaehollandiae*).

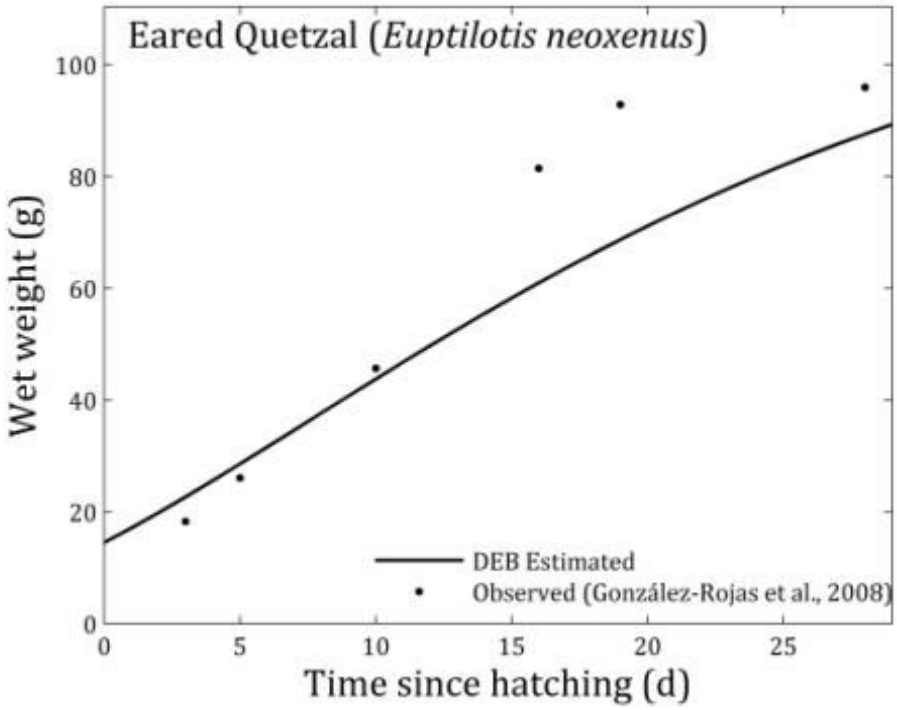

Figure 2.32 – Observed and DEB estimated wet weight growth curve for the Eared Quetzal (*Euptilotis neoxenus*).

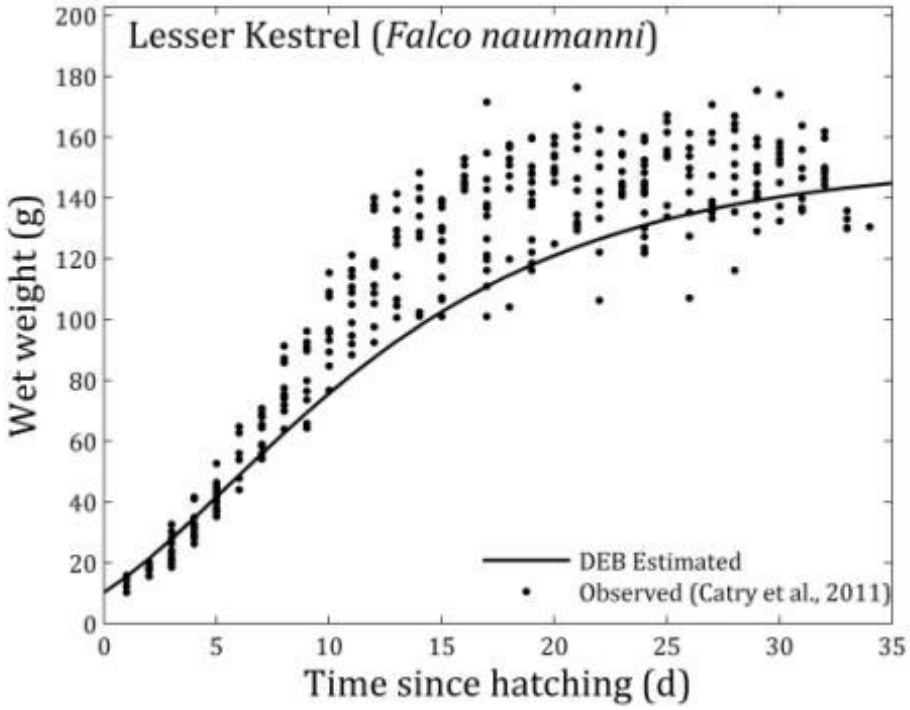

Figure 2.33 – Observed and DEB estimated wet weight growth curve for the Lesser Kestrel (*Falco naumanni*).

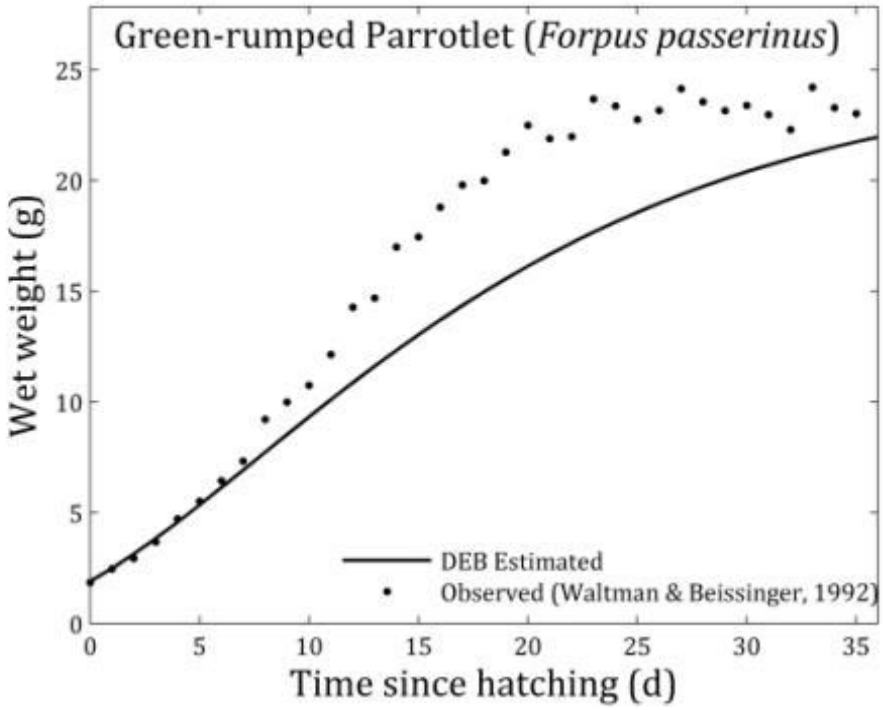

Figure 2.34 – Observed and DEB estimated wet weight growth curve for the Green-rumped Parrotlet (*Forpus passerinus*).

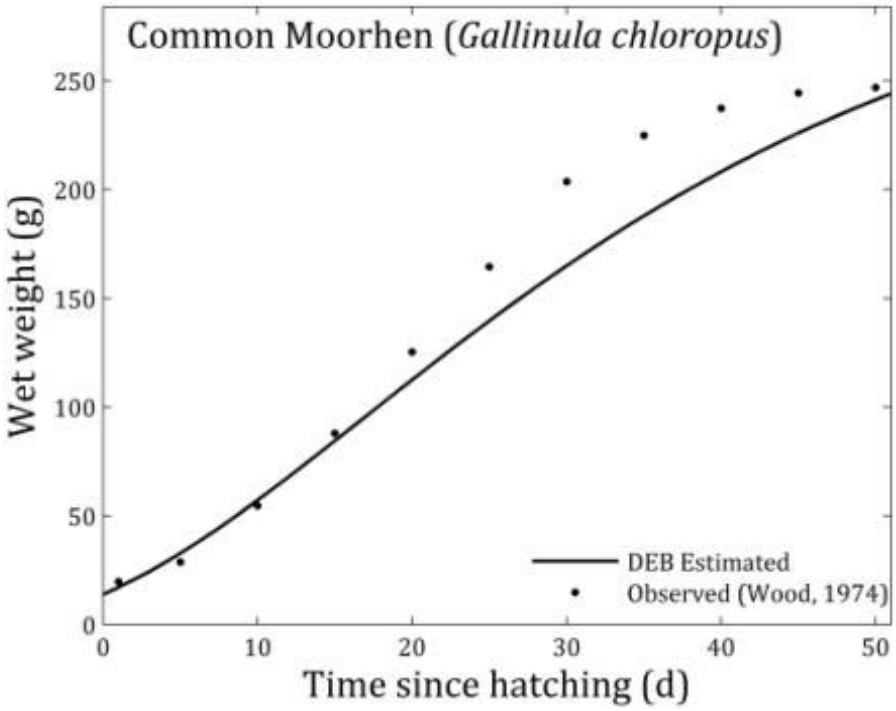

Figure 2.35 – Observed and DEB estimated wet weight growth curve for the Common Moorhen (*Gallinula chloropus*).

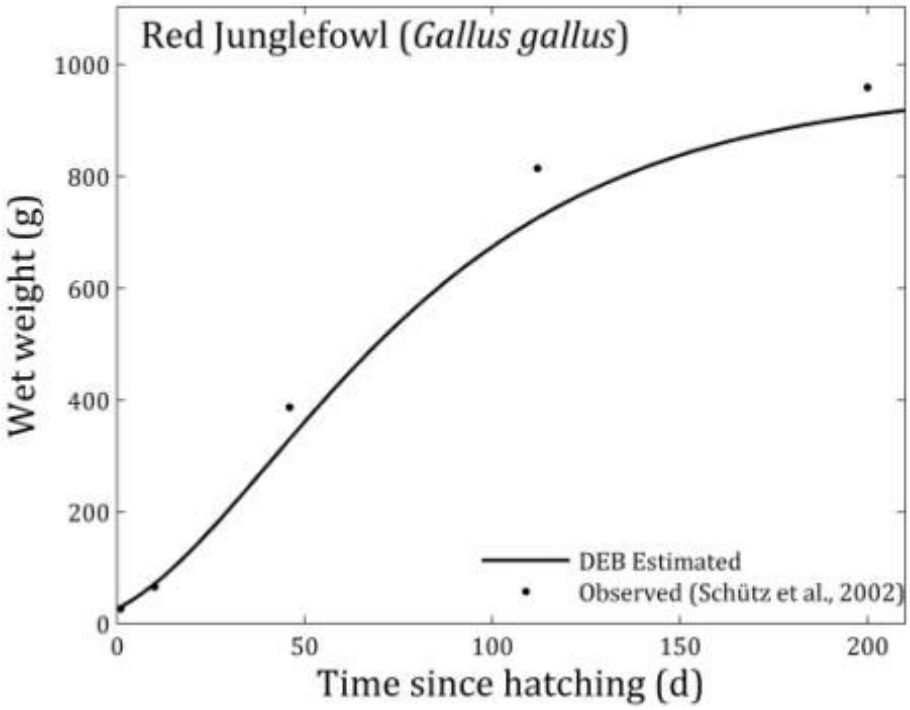

Figure 2.36 – Observed and DEB estimated wet weight growth curve for the Red Junglefowl (*Gallus gallus*).

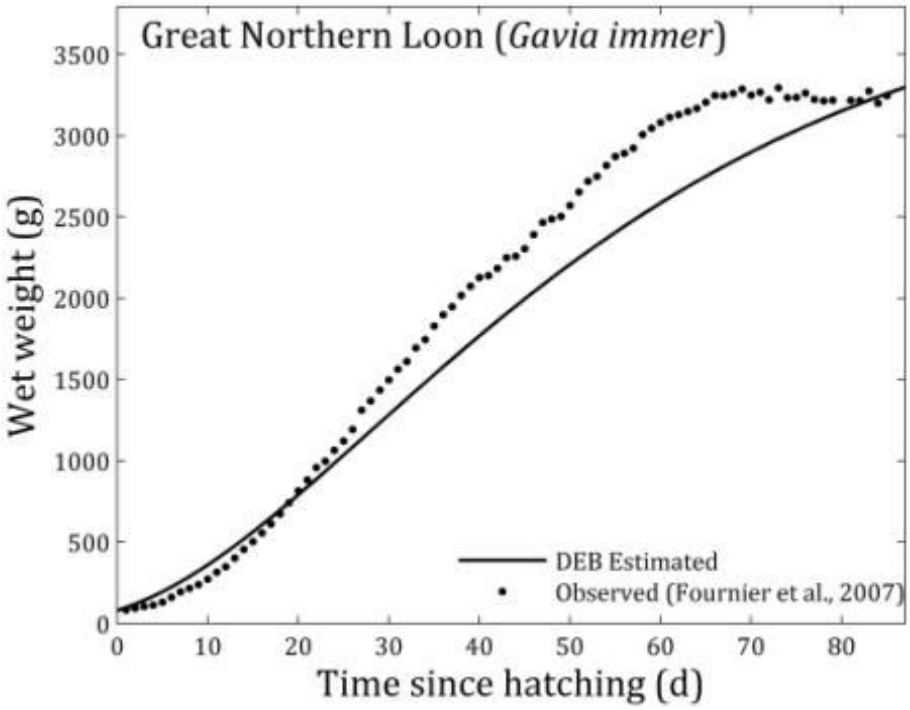

Figure 2.37 – Observed and DEB estimated wet weight growth curve for the Great Northern Loon (*Gavia immer*).

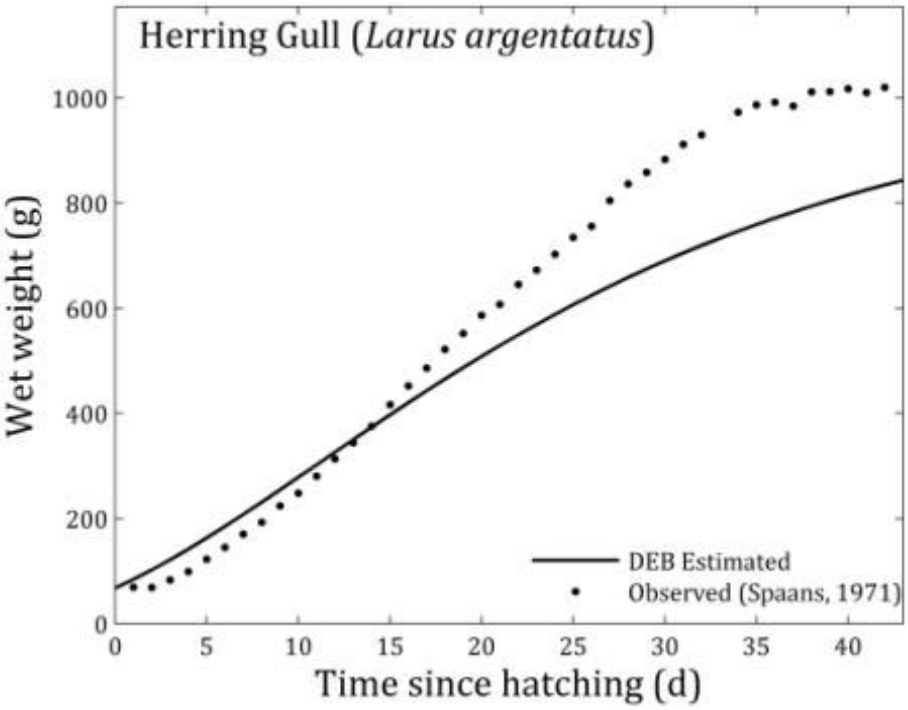

Figure 2.38 – Observed and DEB estimated wet weight growth curve for the Herring Gull (*Larus argentatus*).

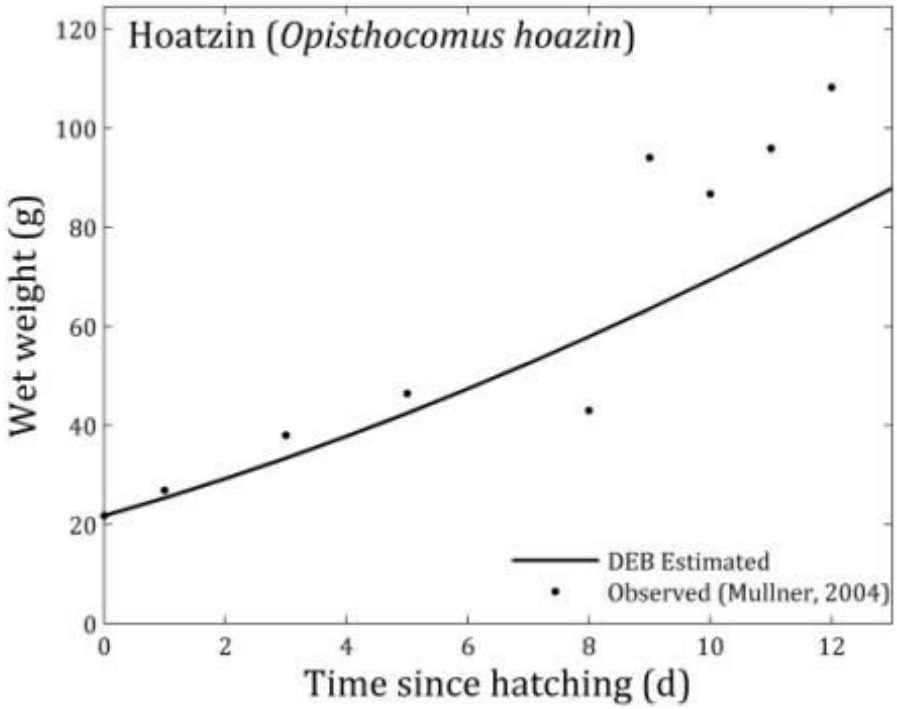

Figure 2.39 – Observed and DEB estimated wet weight growth curve for the Hoatzin (*Opisthocomus hoazin*).

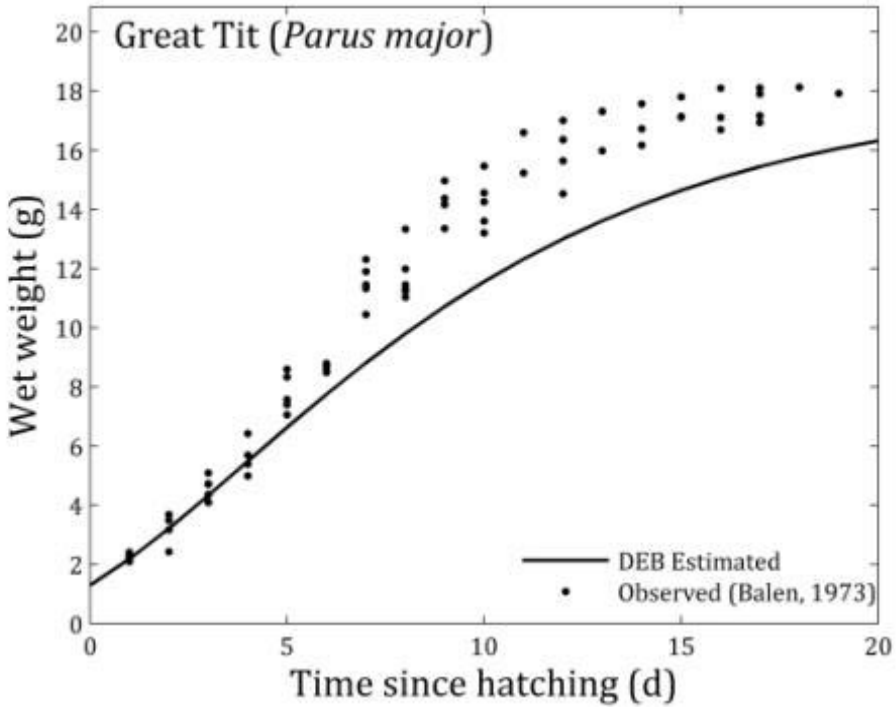

Figure 2.40 – Observed and DEB estimated wet weight growth curve for the Great Tit (*Parus major*).

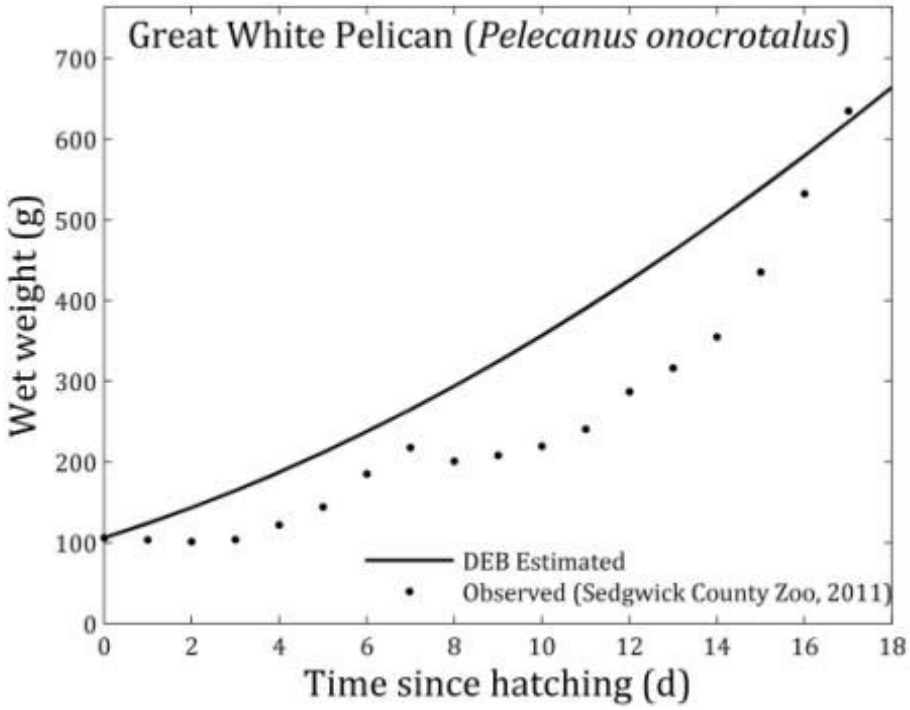

Figure 2.41 – Observed and DEB estimated wet weight growth curve for the Great White Pelican (*Pelecanus onocrotalus*).

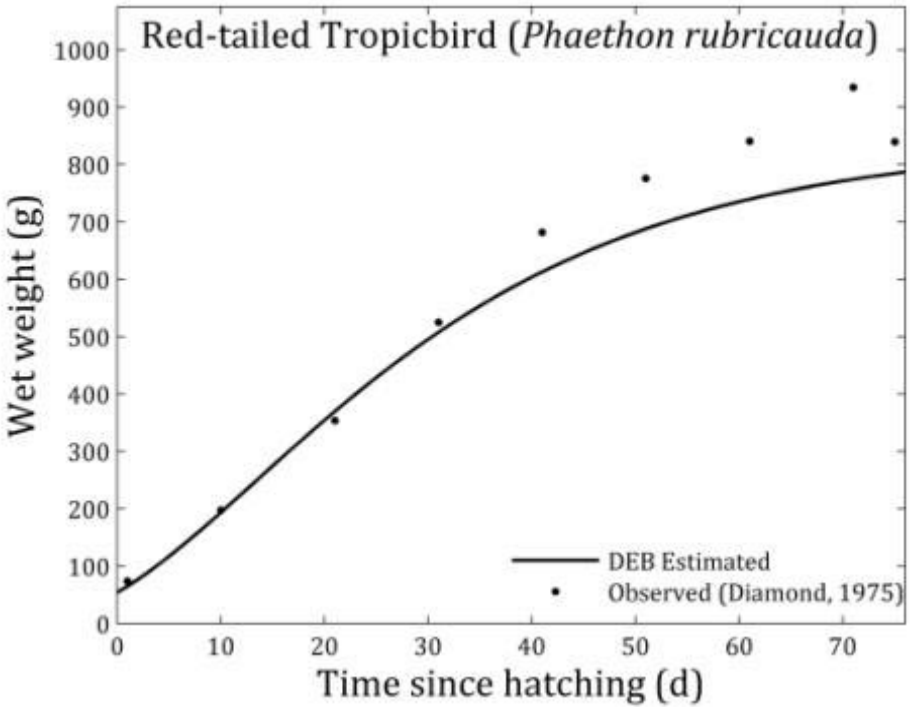

Figure 2.42 – Observed and DEB estimated wet weight growth curve for the Red-tailed Tropicbird (*Phaethon rubricauda*).

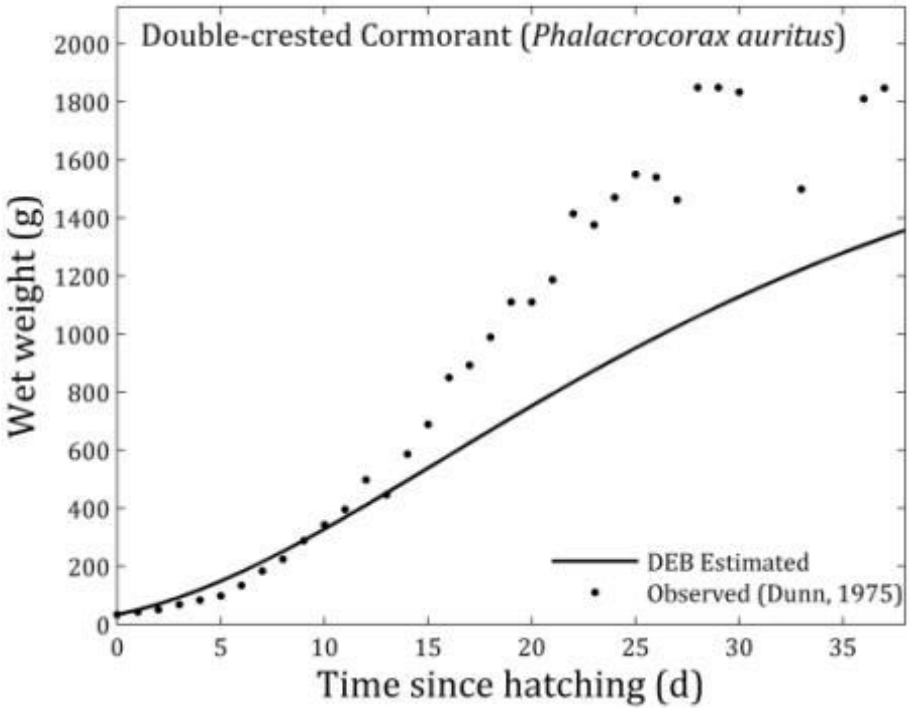

Figure 2.43 – Observed and DEB estimated wet weight growth curve for the Double-crested Cormorant (*Phalacrocorax auritus*).

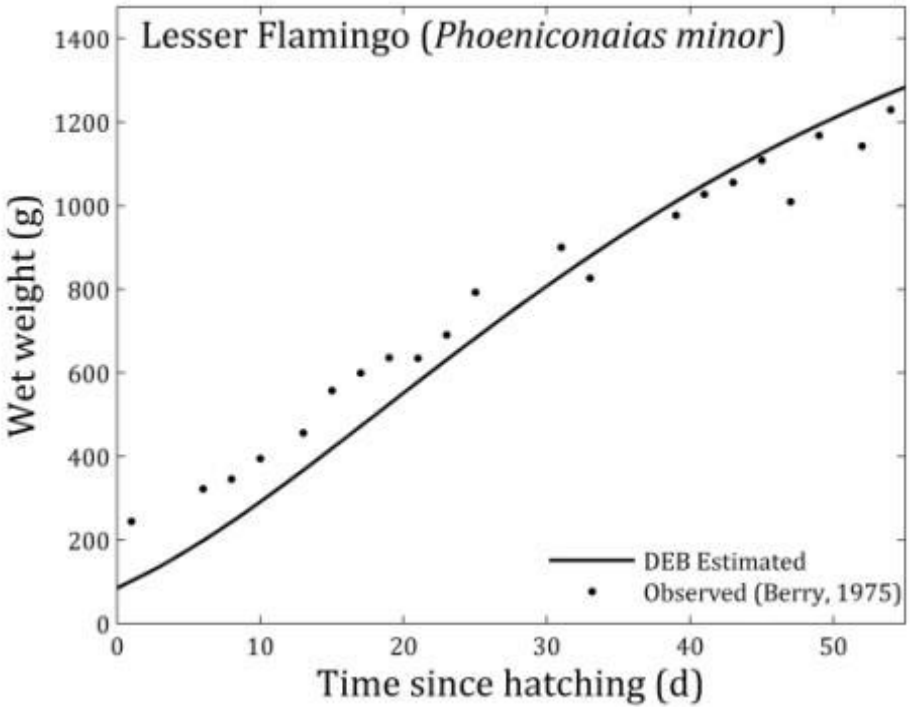

Figure 2.44 – Observed and DEB estimated wet weight growth curve for the Lesser Flamingo (*Phoeniconaias minor*).

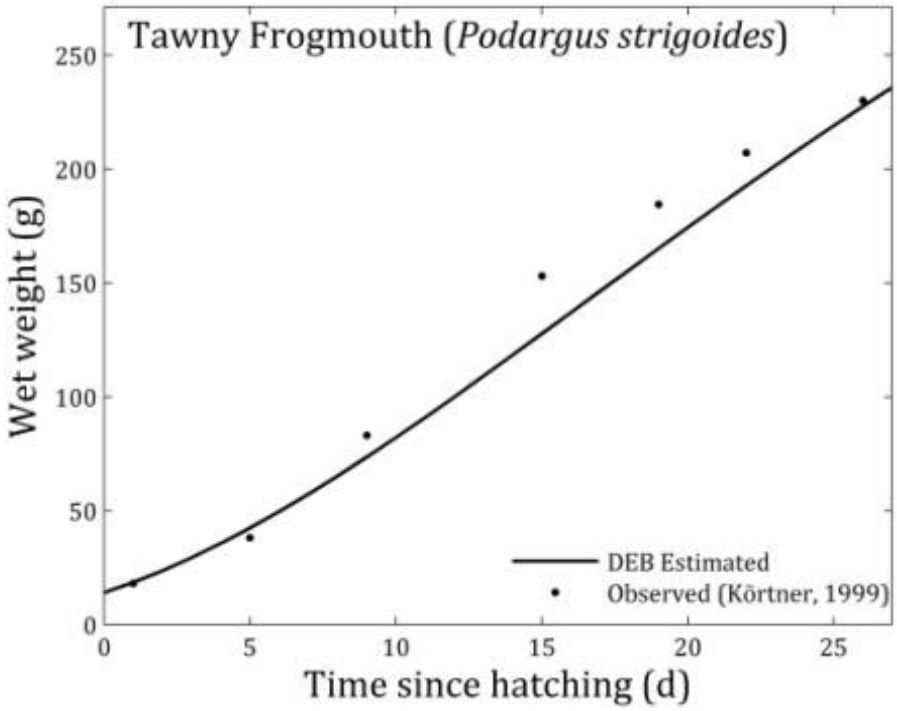

Figure 2.45 – Observed and DEB estimated wet weight growth curve for the Tawny Frogmouth (*Podargus strigoides*).

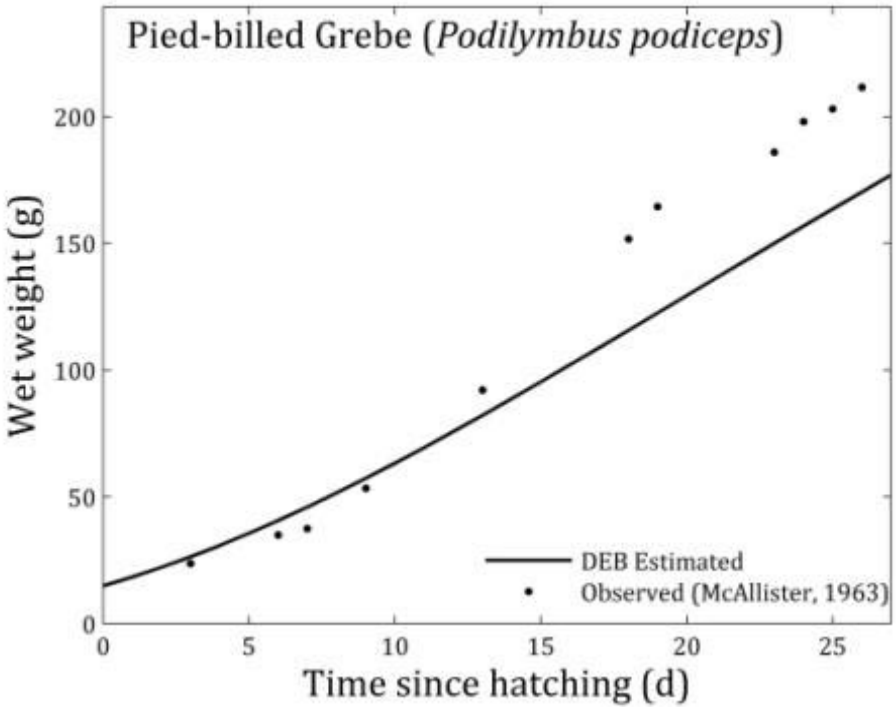

Figure 2.46 – Observed and DEB estimated wet weight growth curve for the Pied-billed Grebe (*Podilymbus podiceps*).

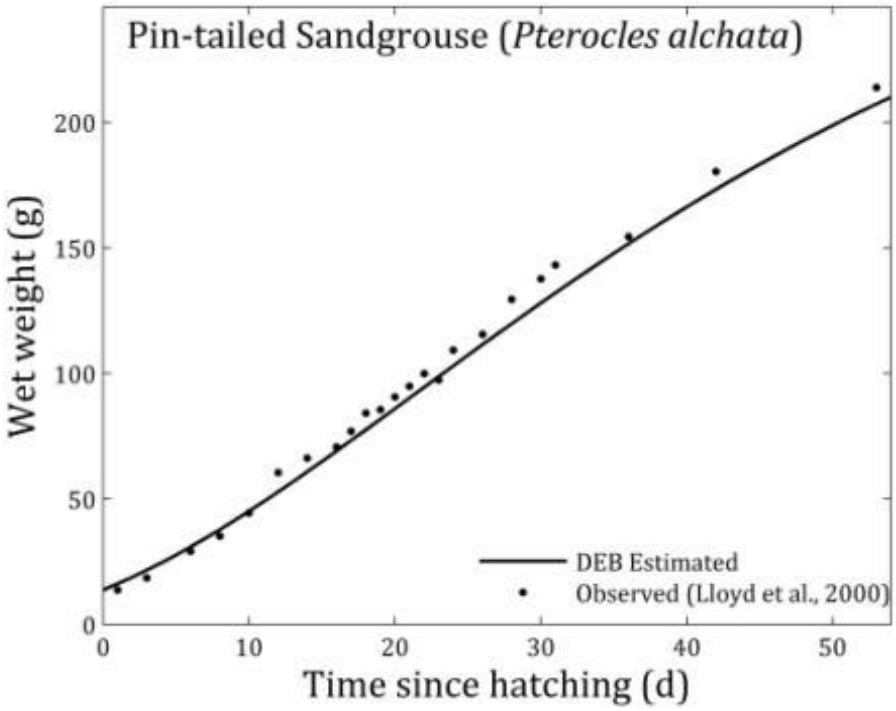

Figure 2.47 – Observed and DEB estimated wet weight growth curve for the Pin-tailed Sandgrouse (*Pterocles alchata*).

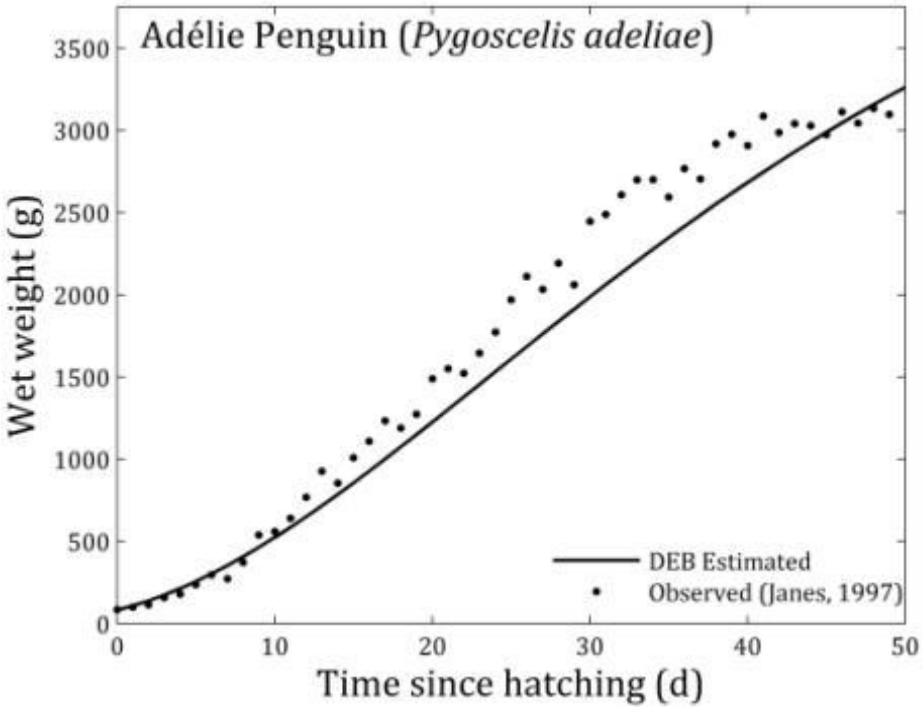

Figure 2.48 – Observed and DEB estimated wet weight growth curve for the Adélie Penguin (*Pygoscelis adeliae*).

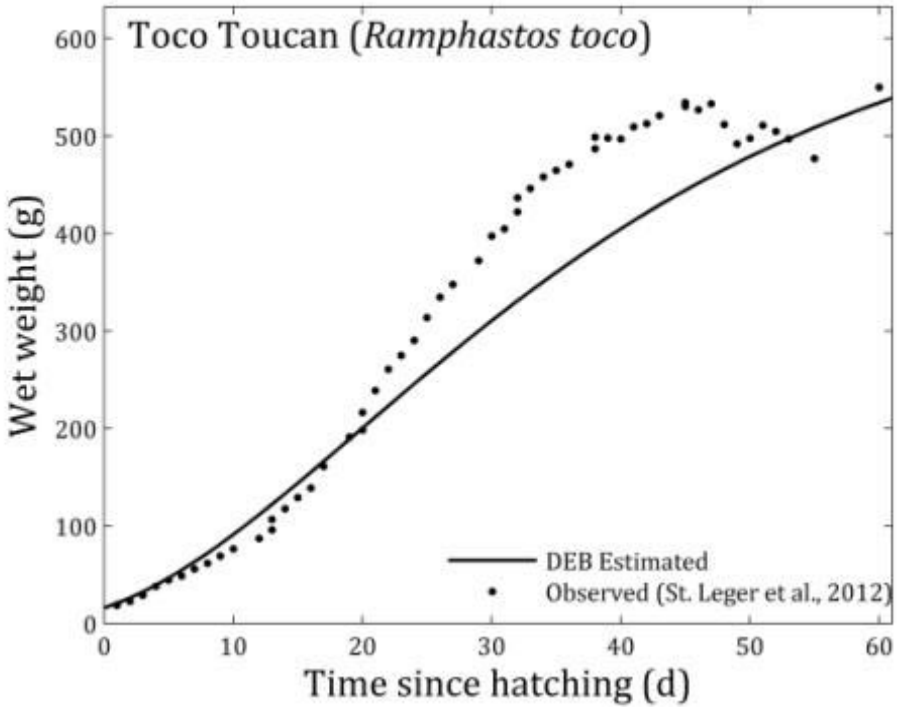

Figure 2.49 – Observed and DEB estimated wet weight growth curve for the Toco Toucan (*Ramphastos toco*).

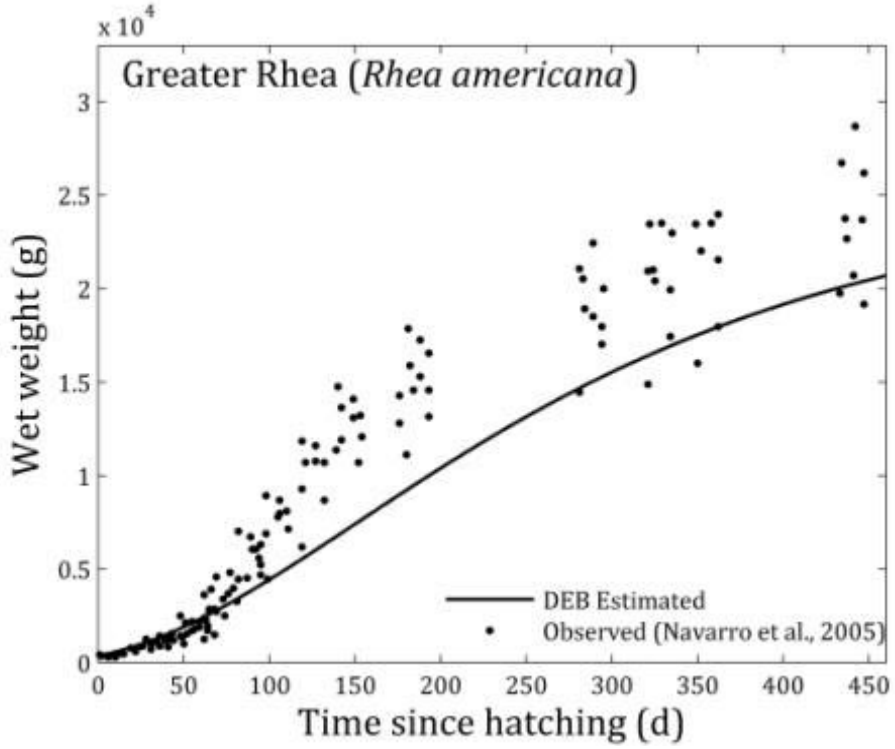

Figure 2.50 – Observed and DEB estimated wet weight growth curve for the Greater Rhea (*Rhea americana*).

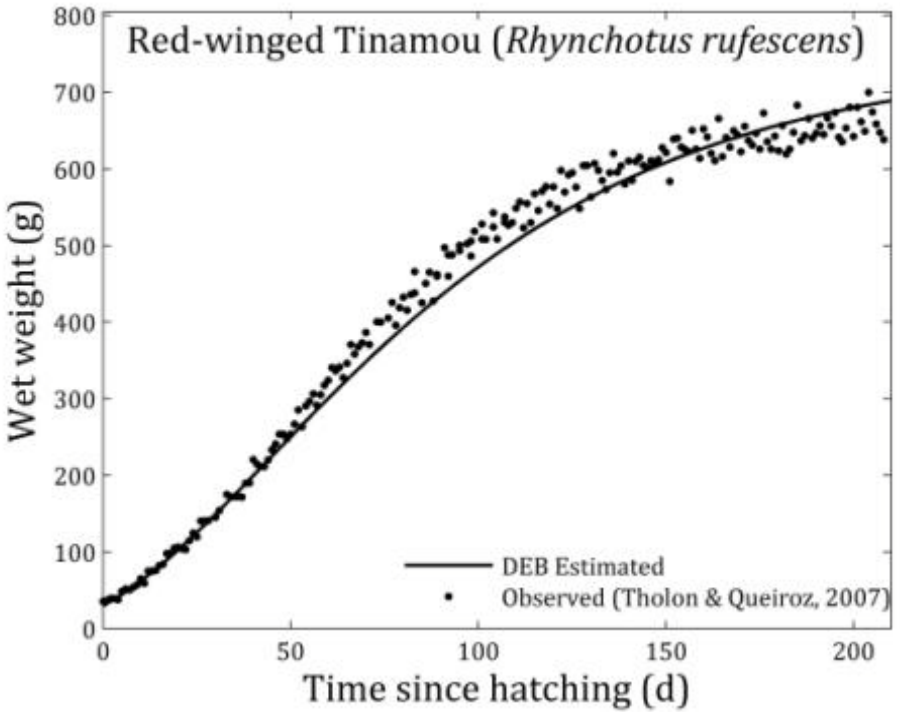

Figure 2.51 – Observed and DEB estimated wet weight growth curve for the Red-winged Tinamou (*Rhynchotus rufescens*).

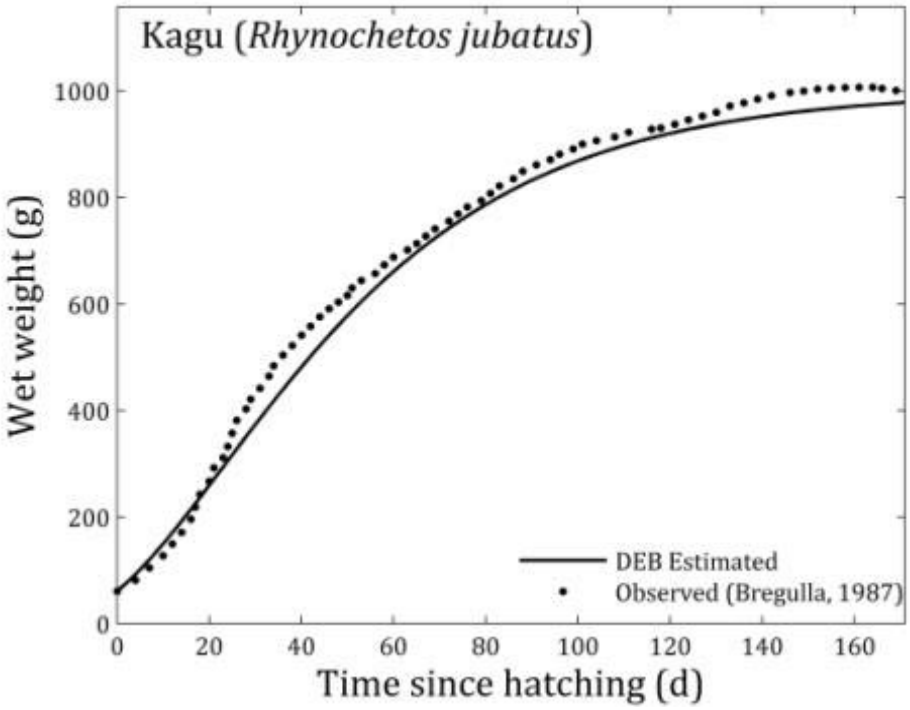

Figure 2.52 – Observed and DEB estimated wet weight growth curve for the Kagu (*Rhynochetos jubatus*).

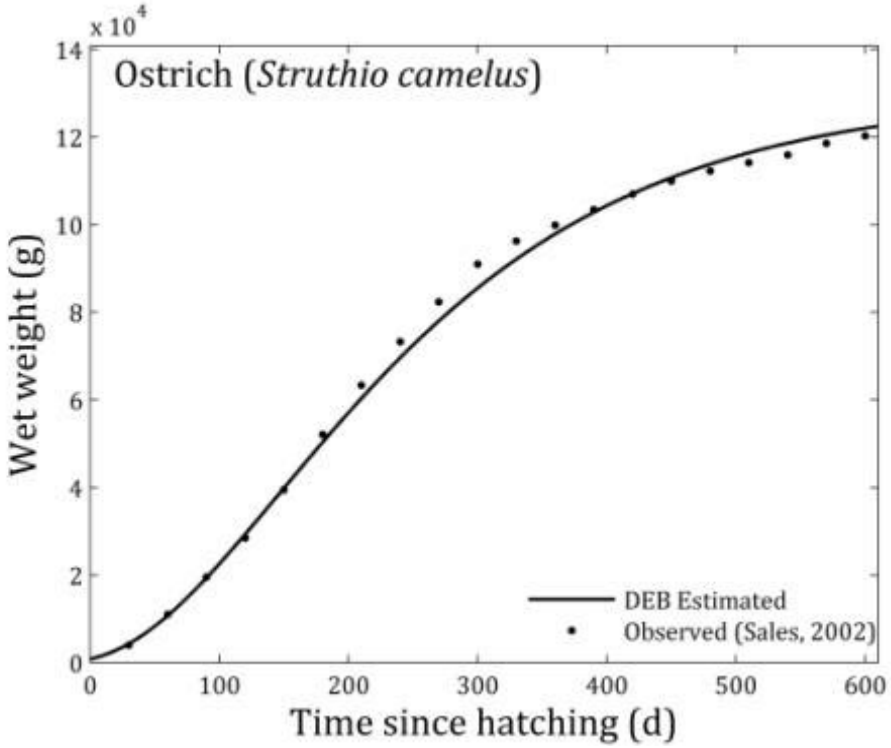

Figure 2.53 – Observed and DEB estimated wet weight growth curve for the Ostrich (*Struthio camelus*).

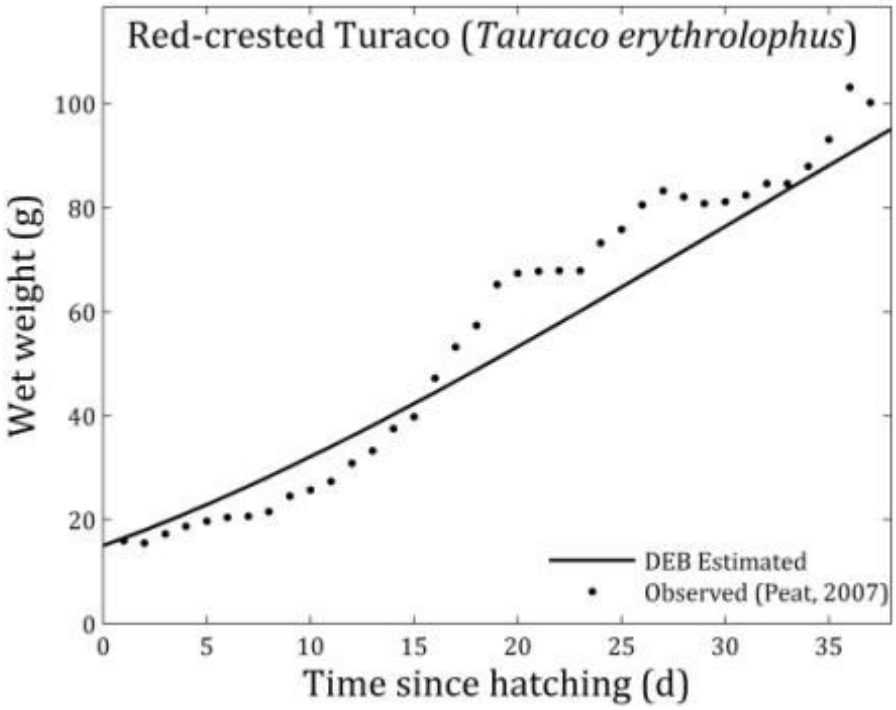

Figure 2.54 – Observed and DEB estimated wet weight growth curve for the Red-crested Turaco (*Tauraco erythrolophus*).

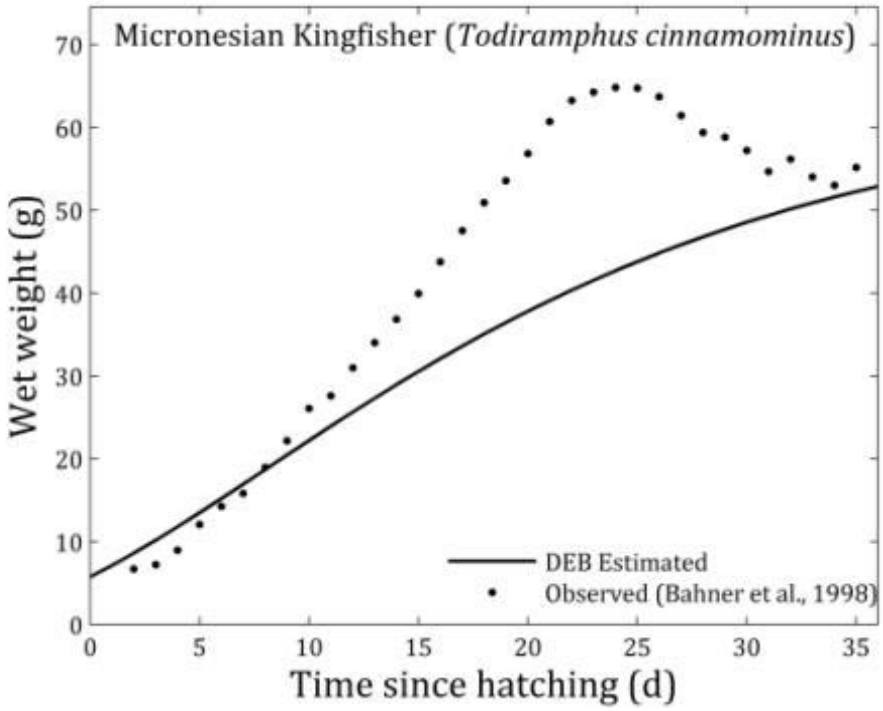

Figure 2.55 – Observed and DEB estimated wet weight growth curve for the Micronesian Kingfisher (*Todiramphus cinnamominus*).

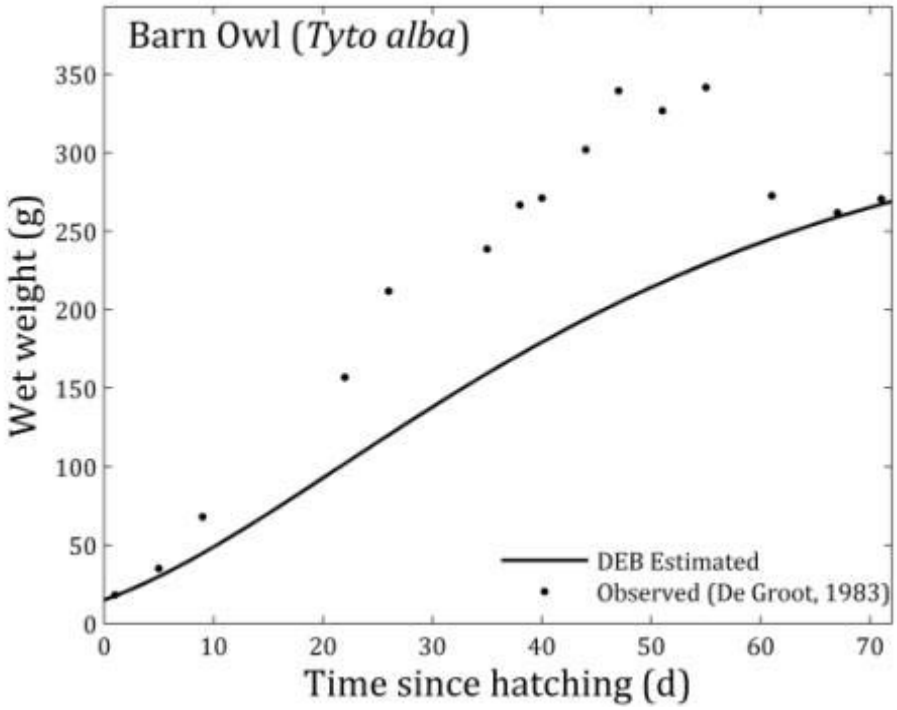

Figure 2.56 – Observed and DEB estimated wet weight growth curve for the Barn Owl (*Tyto alba*).

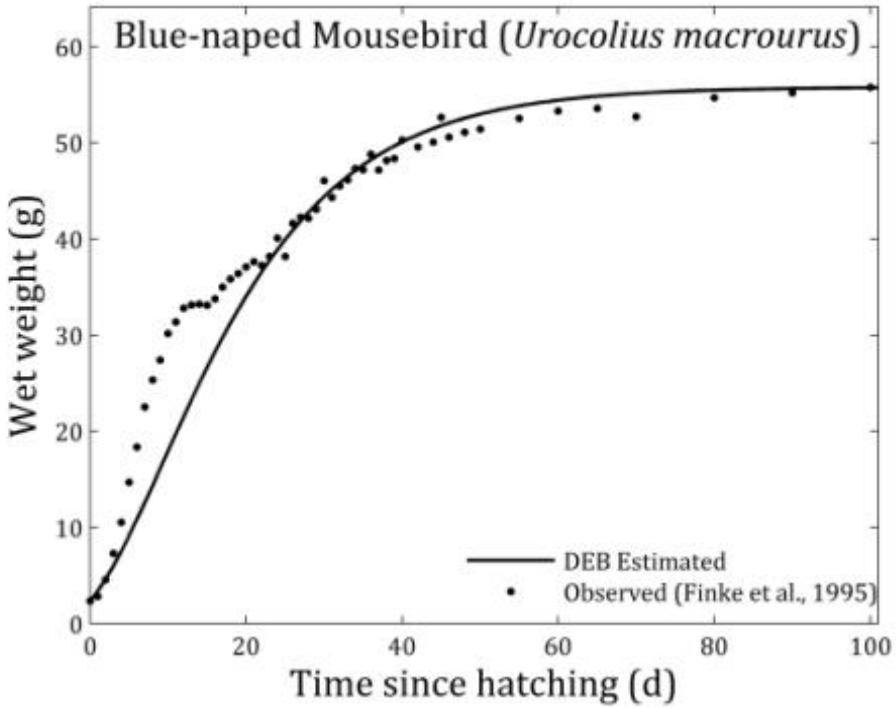

Figure 2.57 – Observed and DEB estimated wet weight growth curve for the Blue-naped Mousebird (*Urocolius macrourus*).

3 Linking metabolism to the life history of birds through the Dynamic Energy Budget (DEB) Theory II: Primary and secondary patterns according to ecological factors

Abstract

The study of life history strategies has been focused on the concept of fitness and on phenotypic indicators such as reproduction costs or survival rates. The identification of relevant metabolic processes and endogenous drivers of variation in the study of life history evolution has been rare. We made use of a set of parameter values previously estimated after the application of the Dynamic Energy Budget (DEB) theory to a sample of 40 species of birds representing the physiological, ecological and biogeographical diversity that currently exists in the group. Based on observations obtained from the scientific literature, we characterized those species according to a set of 13 ecological factors and designed a set of hypotheses describing expectations on how DEB parameters' values could differ according to each ecological factor. In order to test these hypotheses, the relevant primary and compound DEB parameters were plotted and the primary and secondary patterns were analysed individually. The adequate statistical tets were used to assess the relevant correlations and significant differences between different categories of species. A multiple regression analysis was used to explore which factors explained the distribution of values beyond the effect of body size. We found significant differences between two or more categories of bird species for every factor considered. The distribution of values observed for many DEB parameters was significantly explained by body size. These included parameters expected to scale with the ultimate structural length, such as the cumulated energy invested in maturation or the initial egg mass, but also parameters that were not expected to scale with body size, such as the somatic maintenance costs and energy conductance. The most relevant ecological factors to explain the distribution of DEB parameters' values were related to the hatchling development type, migratory status and phylogeny. Strong positive correlations between the reserve mobilisation rate, somatic maintenance costs, von Bertalanffy growth rate and dry mass-specific respiration values are consistent with the waste-to-hurry strategy, with somatic maintenance costs increasing as a response to increased production and growth rates, ultimately determining the evolution of altriciality from earlier, precocial ancestors. These correlations, coupled with the effect of body size, support the hypothesis of a miniaturization trend across the evolution of the Neognathae, as previously suggested. Finally, we demonstrated how the DEB theory allows us to understand apparent trade-offs between life history traits such as the reproduction rate and the egg size, and how these trade-offs actually emerge from specific metabolic constraints quantified and represented by DEB parameters and properties.

Keywords

Dynamic Energy Budget (DEB) theory; life history traits; birds; physiology; metabolism; trade-offs

3.1 Introduction

3.1.1 Initial remarks

The study on the life history of organisms and the evolution of life history strategies can easily be traced back to the beginning of the 20th century (Kunstler, 1900). Fisher (1930) published one of the first landmark studies aiming to describe the drivers and the processes of life history evolutionary change, exploring the genetic implications of natural selection.

The main focus of life history theory has been the concept of fitness and the reproductive consequences associated with different life history strategies. In fact, reproductive costs expressed for instance through clutch size, when studying birds, were among the first indicators to be adopted (Cody, 1966; Lack, 1948, 1947; Moreau, 1944) and remained as the main subject in most of the studies dealing with the evolution of life histories throughout the following decades (Lack, 1968; Lindén and Møller, 1989; Lindström, 1999; Monaghan and Nager, 1997; Partridge and Harvey, 1988; Sæther, 1988) along with other observable consequences of life history change such as population dynamics and survival rates (Cole, 1954; Lack, 1954; Lindström, 1999).

As the study of avian life history evolution has continued to develop (Dobson, 2012; Martin, 2004; Partridge and Harvey, 1988) two fields of research have been particularly explored aiming at the identification and characterization of: a) global patterns and b) sources or drivers of variation.

Gadgil & Bossert (1970) elaborated on the adaptive nature of life histories to explain the existence of patterns and since then other authors described patterns across different latitudes, geographical elements and climates (Olson et al., 2009).

Regarding the sources of life history variation, these have been early on classified as being either environmental or genetic, referring to their exogenous or endogenous nature (Gadgil and Bossert, 1970). Among the different exogenous drivers explored in literature are food and resource availability (Lack, 1968; Martin, 1987), predation pressure (Lack, 1968; Martin, 1993, 1992), nest location (Martin, 1995), sibling competition (Royle et al., 1999), behavioural traits such as territoriality (Newton, 2003) and population dynamics or taxonomic turnover (Olson et al., 2009). Lindén & Møller (1989) reviewed the covariation of life history traits with each other and other ecological factors, focusing on reproduction costs. These costs continued to be the main focus when addressing the effect of exogenous drivers (Ricklefs, 1996, 1991). Recently Ellis *et al.* (2012) reviewed the study of environmental pressures and their effects at the individual level but using stress a physiological indicator instead of the reproduction costs.

Stearns (1976) was one of the first authors to point out that specific combinations of life history traits would occur in particular sets of circumstances and recently Dobson (2012) referred to the cases of hummingbirds and petrels, which have different body sizes, diets and habitats, but exhibit similarly low reproductive rates (which they attribute to nectar feeding and pelagic foraging, respectively), as examples illustrating that different combinations of life history traits could lead to similar life history patterns (such as the reproductive rates), an insight in which the author supports the "lifestyle hypothesis".

Despite all the research conducted on exogenous drivers as well as on the genomics of birds, the existence of relevant processes taking place at the physiological scale was not so readily

addressed and has been harder to study. Notwithstanding, several studies continue to underscore the necessity to advance the study of the physiological processes or proximate mechanisms that may help to understand the observed diversity in the life history traits of organisms in general (Partridge and Harvey, 1988) or birds in particular (Monaghan and Nager, 1997). Studying these processes and the constraints they impose may reveal how the current phenotypic plasticity and trade-offs (Zera and Harshman, 2001), associated with certain life history traits, evolved in birds under the influence of different environmental selective pressures (Martin, 2004). Recently, the need to include mechanistic approaches to physiology and metabolism in order to link environmental change to ecological patterns has also been highlighted for conservation purposes (Seebacher and Franklin, 2012).

The mechanisms of energy intake, assimilation, allocation and use haven't been so frequently explored when addressing the evolution of life histories probably due to the extra difficulty of describing and measuring metabolism and metabolic processes.

In a previous article (Teixeira et al., 2015) the Dynamic Energy Budget (DEB) theory was applied to a sample of 40 (forty) species of birds, selected from forty different Orders, designed to capture diversity at the phylogenetic and ecological scales, including the full range of body sizes. The DEB theory is a metabolic theory that complies with the laws of thermodynamics, unifying traits that are common to all organisms and linking different levels of biological organisation (cells, organisms and populations) (Kooijman, 2010a; Kooijman et al., 2008). The theory uses simple quantitative and mechanistic rules that describe the uptake and use of energy and nutrients (substrates, food, light), the organisation of metabolism and the consequences for physiological organisation throughout the life cycle of organisms (Sousa et al., 2010, 2008).

With the application of DEB theory, the difference between species can be reduced to differences in a single set of parameter values (Table 3.1). Some of these parameters represent metabolic processes that are not easily measured. However, we hypothesized that these processes may correspond to the proximate mechanisms that mediate the effect of environmental selective pressures on life history traits as well as to the physiological constraints that determine the way organisms respond to change at the individual or evolutionary scales. In the referred article (Teixeira et al., 2015), the values for the core DEB parameters were estimated for all the species in the sample. The average values observed for the DEB parameters, which have explicit biological meaning, and their different degrees of variation allowed for some insights regarding the way metabolism may have constrained the life history traits of birds.

The covariation method (Lika et al., 2011a), through which the DEB parameters were estimated, does not imply any particular selective pressure and therefore any deviations from what is physically expected, and the significant differences we may consequently observe between groups of birds, should help us understand how different factors and their respective selective pressures may have influenced the evolution of birds and shaped the current diversity.

The standard DEB model describes the ontogeny of an organism through the dynamics of three state variables – structure ($V = L^3$), reserve (E) and maturity (E_H) – using a set of 'primary' and 'compound' parameters. Primary parameters are connected to a single underlying process and compound parameters are simple functions of parameters, typically depending on several underlying processes.

DEB parameters can also be classified as 'core' or 'auxiliary'. Core parameters are linked to underlying assumptions of DEB theory and relate directly to processes that control the state variable dynamics, which are of an abstract nature. Auxiliary parameters link these abstract variables to quantities that can be measured directly (e.g., length, weight, respiration, etc).

Finally, DEB parameters can also be classified as 'intensive' or 'design' according to their physical meaning and relationship with body size. Intensive parameters are independent of body size. Design parameters co-variate with structural body length. The appropriate ratios of design parameters can also be intensive.

In DEB theory the use of scaling relationships includes body size as a result of underlying processes and not as an independent variable with which eco-physiological properties are regressed empirically (as in allometric relationships). Allometry is not used in DEB theory but physiological quantities (e.g., body weight) and processes (e.g., respiration) are functions of parameters. Inter-species comparisons are performed using the 'zoom factor' – the ratio between each species maximum structural body length (L_m) and that one of a reference species (which may generally be equal to 1 cm). The maximum structural body length is a compound parameter in itself, calculated from other parameters. Several primary and secondary scaling relationships rely on the way DEB primary and compound parameters relate to structural length and therefore theoretical expectations emerge whenever we compare species with differences in length.

In the present article our goal was to make use of the previously estimated DEB parameter sets, to characterize those species according to a set of 13 different ecological factors and to investigate how the variation in the DEB parameters may be differently associated with these ecological factors.

The first factor considered in this study simply groups species according to the Superorder in which they are classified and brings in an element of basal phylogenetic divergence ('Superorder'). The second factor is related to the type of development observed in nestlings up until they reach autonomy or puberty ('Development type'). The third factor splits the species according to their flight capacities ('Flight'). The four following factors are related to reproductive behaviour and include the different mating systems observed in modern birds ('Mating system'), the differential amount of parental care dedicated by one or more adults during the nestling stage ('Parental care'), the level at which the nest is built ('Nest level') and the type of nest involved ('Nest type'). The eight ecological factor of this study regards the ability to exhibit torpor as a strategy to deal with physiological activity. The ninth factor considered in this study simply groups species according to their main foraging habitat ('Foraging habitat'). The tenth factor is related to migratory behaviour ('Migratory status'). The eleventh factor separates species according to their predominant diet ('Diet'). The twelfth factor groups species according to the main climatic regime in the regions they inhabit ('Climate'). Finally we also included a factor related to each species conservation status ('Conservation status').

Taking previous research into consideration, a few hypotheses are proposed for each factor.

Table 3.1 – The core parameters of the standard DEB model and their respective summarized descriptions. More details are available in Lika et al. (2011).

Parameter	Abbreviation	Summarized description
Surface-specific maximum assimilation rate (J d^{-1} cm^{-2})	$\{\dot{p}_{Am}\}$	Controls the assimilation of energy from ingested food.
Zoom factor (-)	z	Controls the maximum length via the surface-specific assimilation.
Maximum surface-area-specific searching rate (dm^3 d^{-1} cm^{-2})	$\{\dot{F}_m\}$	Controls food intake if food is not abundant and has no effect at abundant food.
Digestion efficiency (-)	κ_X	Specifies the fraction of energy in food that is fixed in reserve.
Defecation efficiency (-)	κ_X^p	Specifies the fraction of energy in food that ends up as faeces.
Energy conductance (cm d^{-1})	$\dot{v}$	Controls the reserve mobilisation.
Allocation fraction to soma (-)	κ	Controls the allocation of mobilised reserve to somatic maintenance and growth as opposed to maturity maintenance and maturation of reproduction.
Reproduction efficiency (-)	κ_R	Fraction of reserve allocated to reproduction that is fixed in the reserve of offspring.
Volume-specific somatic maintenance rate (J d^{-1} cm^{-3})	$[\dot{p}_M]$	Controls the sink of reserve linked to structural volume, mostly due to turnover of structure, behaviour and transport.
Surface-specific somatic maintenance rate (J d^{-1} cm^{-2})	$\{\dot{p}_T\}$	Controls the sink of reserve linked to structural surface area.
Maturity maintenance rate coefficient (d^{-1})	$\dot{k}_J$	Controls the sink of reserve linked to maturity.
Specific cost for structure (J cm^{-3})	$[E_G]$	Reserve energy required to synthesize a unit volume of structure.
Maturity at birth (J)	E_H^b	Controls the timing of and the size at birth, i.e., the moment assimilation is switched on.
Maturity at fledging (J)	E_H^x	Controls the timing of fledging, i.e., the moment at which self-feeding starts.
Maturity at puberty (J)	E_H^p	Controls the timing of and the size at puberty, i.e., the moment at which investment into maturation is re-directed to reproduction.
Weibull ageing acceleration (d^{-2})	$\ddot{h}_a$	Controls the mean life span in a way that hardly depends on food density (dilution by growth cancels the increased respiration).

3.1.2 Hypotheses

3.1.2.1 Superorder

The Superorder factor groups species according to which of the two living clades of birds they are classified into, namely the Palaeognathae and the Neognathae. The Neornithes is formed from these two clades. One species from each of the forty Orders of modern birds are included in the sample analysed in this study: 35 species from the Superorder Neognathae and 5 from the Palaeognathae, according to the classification system adopted in the World Bird List of the International Ornithologists' Union (Gill and Donsker, 2012).

Considering that three of the species of Palaeognathae included are among the biggest and heaviest birds in the world, the ratites (the Ostrich, *Struthio camelus*, the Greater Rhea, *Rhea Americana*, and the Emu, *Dromaius novaehollandiae*), differences in body size are expected to play a significant role when comparing the two clades of birds.

Correlations between growth rates and body mass have been frequently observed (McNab, 2012, 2009, 1988; Ricklefs, 1968; Ricklefs et al., 1998; Symonds, 1999). Originally, Ricklefs (1968) stated that such correlations suggested the occurrence of interactions between body mass and certain physiological functions and highlighted the importance of evolutionary forces for the definition of growth patterns. Later, Ricklefs *et al.* (1998) observed that the relationship between growth rate and body mass accounted for 63% of the overall variation in their data and considered body mass to be the strongest factor regarding the variation of growth rates in birds. Symonds (1999) suggested that growth rates are constrained by metabolism, especially in small species, and McNab (2012) pointed out that at smaller masses continuous endothermy relies on higher basal metabolic rates. McNab (2012) also noted that an appreciable residual variation in growth rates was not related to body mass but other uncertain metabolic factors. DEB theory predicts that the von Bertalanffy growth rate at abundant food should decrease with the ultimate structural body length of species. Several other DEB parameters are expected to increase with body size, such as the energy investment in maturity, the surface-specific assimilation rate and the maximum reserve capacity.

It is also important to consider that the three ratites included in the Palaeognathae are flightless. The two other Palaeognathae species comprise the flightless North Island Brown Kiwi (*Apteryx mantelli*) and the almost flightless example of the Tinamiformes, the Red-winged Tinamou (*Rhynchotus rufescens*). Therefore, despite the presence of several other flightless or almost flightless species of Neognathae in the sample, there is a possible correlation between the differences observed between the two clades of birds and the capacity to fly. The expectations regarding this capacity are referred further ahead.

Based on these observations, the first hypothesis to consider in this study is the following:

Hypothesis 1: differences between the Palaeognathae and the Neognathae should reflect mainly the effect of body size.

3.1.2.2 Development type

This factor groups species according the kind of development pattern observed in the nestlings, typically classified in the altricial-to-precocial spectrum. This is one aspect of avian life history that has previously been commented in the context of DEB theory. Acknowledging this theory in their study, Konarzewski *et al.* (1998) pointed out that differences observed in

the altricial-to-precocial spectrum of development types should find expression in the DEB parameters themselves.

Other observations regarding development patterns have been published and are useful to consider. Ricklefs (1968) observed slower growth rates in precocial birds and Ricklefs *et al.* (1998) concluded that these differences in growth rate among species should represent compromises between environmental factors (that influence mortality) and internal constraints. Since then other studies suggested that differences in growth rates should be relevant to the definition of the altricial-to-precocial spectrum. Karlsson & Lilja (2008) observed that the higher the embryonic growth rate, the less ossified the skeleton is at hatching. Starck & Ricklefs (1998) pointed out that functional differences between altricial and precocial chicks could be responsible for differences in their postnatal growth rates and Klasing (1999) observed a faster embryonic growth rate of the digestive tract in altricial birds, allowing for a higher capacity to receive and digest large quantities of food after hatching and henceforth sustaining higher postnatal growth rates. Gebhardt-Henrich & Richner (1998) stated that at least some of the variation in growth rates needs to be heritable in order to allow evolutionary change. By studying the skeleton, Dyke & Kaiser (2010) concluded that relative egg sizes and available development types were constrained in many early birds because the oviduct diameter was limited by the presence of pubic fusion. The same authors stated that larger eggs could actually be necessary for the embryonic development of precocial birds. Taking all of this into consideration, the second hypothesis to consider in this study is the following:

Hypothesis 2: altricial bird species should exhibit higher growth rates, lower investment in maturity and smaller eggs than precocial species.

3.1.2.3 Flight

In DEB theory locomotion costs are included in the somatic maintenance costs. Several studies have suggested that flying activities contribute significantly for this budget (Nudds and Bryant, 2000; Raveling and LeFebvre, 1967; Torre-Bueno and Larochelle, 1978; Weimerskirch et al., 2014). The average heart rate of resting adults of the Wandering Albatross has been estimated to be about 0.67 of the value obtained during flight (including the expensive lifting-off from water) (Teixeira et al., 2014). Large pectoral muscles and heart masses, as well as other possible traits related to flight, may illustrate the cost of this activity, which may increase the basal metabolic rate to a value 35% greater than those measured in flightless species, according to McNab (2012). In DEB theory, a positive correlation between the somatic maintenance costs and the von Bertalanffy growth rate is expected. Considering that there is a negative correlation between the latter and sexual maturity, the same correlation is expected to occur regarding the somatic maintenance costs. Considering all of these observations, our third hypothesis is the following:

Hypothesis 3: bird species exhibiting the capacity to fly should have higher somatic maintenance costs and growth rates but reach sexual maturity sooner than flightless bird species.

3.1.2.4 Mating system

Orians (1969) predicted that polygyny should prevail more among precocial birds and Royle et al. (1999) observed a positive association between growth rate and both extra-bond paternity and mating system, indicating that sexual conflict and reduced intrabrood relatedness increases sibling competition and had a positive effect on chick growth rates. However these

authors also state that when there is no intrabrood sibling competition, growth rates should not be affected by the degree of extra-bond paternity (e.g., when there is real monogamy) and that ultimately, the upper limit on growth rates is set by internal, physiological constraints. Considering the observations of these authors and the possible correlation between mating systems and development types, differences in growth rates are expected when comparing mating systems and this constitutes our fourth hypothesis:

Hypothesis 4: monogamous bird species should exhibit higher growth rates than polygamous bird species.

3.1.2.5 Parental care

Studies relating different degrees of parental care and physiology are very rare. For instance, most of the hypotheses suggested to explain the origin and evolution of cooperative breeding in birds rely on behavioural traits, such as kin selection (Stacey and Koenig, 1990) or brood parasitism (Feeney et al., 2013) among others. However, many bird species, particularly altricial ones, are dependent on considerable parental care after they hatch and before they are able to fledge. Considering that this is the period when most or the totality of the post-hatching growth takes place, differences in growth rates may be expected to occur when comparing bird species that have two or more adults (progenitors and/or helpers) providing food and those that are reared by a single progenitor, which constitutes our fifth hypothesis for this study:

Hypothesis 5: hatchlings reared by a different number of adults should exhibit different growth patterns and/or different growth rates.

3.1.2.6 Nest level

Martin (1995) observed significantly higher levels of predation pressure in canopy nests than in ground nests, which also had higher success rates, but no correlation between predation and body size. However, Dyke & Kaiser (2010) stated how changes in traits such as increased parental care and sophisticated nest-building seem to be well illustrated by the current phylogeny of birds and pointed out that these trends could be related to an general decrease in adult size driven by a change of habitat use from simple, open environments to complex three-dimensional structures (tree canopies). Sustained miniaturization has actually been recently suggested as the main trend across the whole evolution of birds from their dinosaurian ancestors (Lee et al., 2014) and flight as well as the ability to colonize arboreal habitats has also been associated to this trend (Benton, 2014). The possible correlations between nest building at higher locations and both body size and parental care suggest that those differences expected to occur due to these two factors, such as differential growth rates, somatic maintenance costs and sexual maturity, are also expected to be observed when considering nest location. Additionally, all of the Palaeognathae species nest on the ground so a correlation between these two factors is very probable. Taking all of these observations into consideration, our sixth hypothesis is the following:

Hypothesis 6: bird species that nest in higher locations should exhibit higher growth rates and somatic maintenance costs and should reach sexual maturity sooner than bird species that build their nests in low locations.

3.1.2.7 Nest type

Bosque & Bosque (1995) observed that native species from islands that use open nests take longer to hatch and fledge than related species from continents, controlling for body mass, but found no difference when considering species that had been recently introduced to islands. For these authors predation was an important selective pressure on the evolution of continental altricial birds. They also observed slower development rates in bird species using closed nests (e.g., holes). Recently, Dyke & Kaiser (2010) stated that more complex nests may represent a response to the thermal issues related to small parental size. These authors also noted that early diverging precocial birds use unsophisticated nests that simply keep their eggs from rolling away. Considering these observations, our seventh hypothesis is the following:

Hypothesis 7: differences regarding the incubation period, fledging and the growth rate are expected to occur between bird species that use open nests and those that use closed nests.

3.1.2.8 Torpor

Torpor corresponds to a state of reduced physiological activity characterized by significantly lower body temperatures and metabolic activity. Previous studies found correlations between the ability to display torpor and factors such as diet, foraging strategy and phylogeny, as well as to body mass and energy expenditure (McNab, 2012). Schleucher (2002) concluded that diet and food availability may be the main factors associated with torpor. McNab (2012) observed that birds with the capacity to exhibit torpor have basal metabolic rates that are higher than those of birds that do not use torpor. These observations regarding higher basal metabolic rates should correspond to higher reserve mobilisation rates and/or higher somatic or maturity maintenance rates, in DEB theory. Taking all of this into consideration, the eighth hypothesis for the present study is the following:

Hypothesis 8: bird species that exhibit torpor should have higher reserve mobilisation, somatic or maturity maintenance rates than species that do not perform torpor.

3.1.2.9 Foraging habitat

Previous studies have concluded that pelagic bird species were up to 40% less productive as regards to reproduction, than other birds (Dobson, 2012; Sibly et al., 2012) and that marine bird species had higher resting and basal metabolic rates then terrestrial species (Bennett and Harvey, 1987; Nagy, 1987). Taking these observations into consideration, our ninth hypothesis is the following:

Hypothesis 9: marine and/or pelagic species should allocate more energy to somatic growth and maintenance but less energy to reproduction than terrestrial ones.

3.1.2.10 Migratory status

Migratory behaviour has been extensively studied and its constraints on metabolism have also been explored (Alerstam, 2011; Gwinner, 1990; Jenni and Jenni-Eiermann, 1988; Jetz et al., 2008; Klaassen, 1996; Nilsson et al., 2011). However, most regulatory mechanisms still remain to be identified, particularly on the physiological level (Bairlein and Gwinner, 1994) and the need to develop mechanistic models to predict migratory behaviour has been recently highlighted (Klaassen et al., 2012). Overall, the evolution of migratory behaviour in birds has been described as driving a continuous optimization effort of energy, time and predation risks (Alerstam and Lindström, 1990; Alerstam, 2011; Lindström and Kvist, 1995).

Many studies have focused on the particular demands that the migratory behaviour has on the physiognomy of birds. Hypertrophy, the development of particularly demanding muscles for flight with substantial aerobic endurance (W. R. Dawson et al., 1983; Klasing, 1999), the ability to perform a widespread deposition of fat and fat-free tissue during migration (Lindström and Piersma, 1993; Rappole, 2013) as well as the capacity for frequent variation in mass observed in nutritional organs and flight muscles during the fuelling–flight cycle (particularly the increase in the gizzard, stomach, intestine and liver to increase energy assimilation and their subsequent reduction to reduce payload and flight costs) (Hedenström, 2008; Newton, 2008), are examples of these demands.

Some studies highlighted the food assimilation efficiency of migratory birds and the ability to quickly make use of the energy stored in body reserves (Hedenström, 1993; McWilliams et al., 2004). The increase of hyperphagia before migration has been characterized as essential for fat deposition. It does not fully account for the complete pre-migratory mass gain observed in sparrows but it has been attributed to an increase in assimilation efficiency (Bairlein and Gwinner, 1994).

Migratory birds, particularly those that perform long distance migrations, have also been previously characterized as having higher basal metabolic rates due to: a) high maximum fuel deposition rates and the metabolic activity of food-processing organs or locomotion activity and respective elevated maintenance costs (Jetz et al., 2008; Lindström and Kvist, 1995), and b) their predominantly cold high-latitude breeding areas or as a result of measurements taken in different moments and circumstances (Jetz et al., 2008).

Taking all of these observations into consideration, our tenth hypothesis for the present study is the following:

Hypothesis 10: migratory bird species exhibit higher allocation fractions of energy to somatic growth, higher reserve mobilisation rates and higher assimilation rates than non-migratory bird species.

3.1.2.11 Diet

The evolution of different dietary habits in birds and the physiological and energetic implications of such evolution has already been explored in previous studies (Kirkwood, 1983; Klasing, 1999; McNab, 1988). However, according to some authors, the relative contribution of diet to metabolic rates in birds has been less explored than in mammals (McNab, 2012) and cause–effect relationships are hard to establish considering the current knowledge on the interactions between the chemical compounds in food and the organism (Schleucher, 2002).

Considering the whole group of birds, there seems to be an almost continuous distribution of digestive-tract morphologies, ranging from the simplest (nectarivores) to the most elaborate (herbivores) but most species are in the middle of this spectrum (e.g., omnivores and insectivores) (Klasing, 1999). Diets that require more enzymatic attack (animal matter and seeds) require large stomachs (despite relatively small lower intestines) with insects constituting a diet of high energy content for birds (18.0 kJ g^{-1} of dry matter) and arthropods allowing for a high utilization efficiency (77%) (Karasov, 1990; Klasing, 1999; Nagy, 1987). However, the small intestine tends to be long in herbivores and granivores and relatively short in carnivores, nectarivores, and frugivores, and some species specialized in digesting plant material (i.e., rich in cell walls) have large ceca for fermentation purposes (Klasing, 1999). It seems clear that anatomically, diets based on material of vegetal origin ("plantivores") and diets based on material of animal origin ("faunivores") can be similarly demanding.

Kirkwood (1983) discussed the existence of upper limits to food intake resulting from gut size as well as assimilation and metabolisation constraints, and Karasov (1990) related the digestive system's efficiency to digesta retention time, hydrolysis, fermentation and assimilation rates and inherently the volume and surface-area of the digestive tract. The latter author observed reduced efficiency in frugivores and an increase in digestive tract volume in herbivores. If plantivores tend to have larger digestive tracts, particularly because of longer small intestines where enzymatic digestion and absorption of the end products of digestion occur (Klasing, 1999), i.e., assimilation takes place over a larger surface, but the amount of energy in the ingested food remains the same, then the differences regarding surface-specific assimilation rates are expected to occur when comparing plantivores and faunivores.

The activity level and locomotion costs need also to be addressed when discussing the diets of birds. Schleucher (2002) suggested that the low metabolic rates found in some frugivores could result not from the food content but from the non-migratory lifestyle of these species. Klasing (1999) pointed out that the capacity for flight and migration allowed birds to forage high quantities of nutritious foods in habitats unavailable for non-flying animals but placed physical limitations – flight places a maximum on body weight of about 12 kg while non-flying birds may grow heavier and carry complex digestive tracts that allow high-fibre herbivorous diets. McNab (2012) also explained the high field energy expenditures of carnivores and insectivores through their intense foraging costs, highlighting the example of swallows that persistently hunt flying insects. According to DEB theory, locomotion costs are included in volume-specific somatic maintenance costs ($[\dot{p}_M]$) (J d^{-1} cm^{-3}) (Kooijman, 2010a).

Taking all of these observations regarding the diets of modern birds, into consideration, our eleventh hypothesis is the following:

Hypothesis 11: plantivore bird species should exhibit lower assimilation rates and somatic maintenance costs than faunivores bird species.

3.1.2.12 Climate

The relationship between climate and metabolism has been explored several times before, particularly focusing on the effects of climate on basal and standard metabolic rates and describing higher rates in cold climates than in warmer ones (Chaffee and Roberts, 1971; Mcnab and Morrison, 1963) even when measurements are independent of body size (Weathers, 1979). Several drivers have been suggested through which climate could exert selective pressure on metabolic processes. Some authors described how increases in the daily energy expenditure could require more expensive metabolic processes, consequently increasing metabolic rates (Daan et al., 1990; Lindström and Kvist, 1995). These authors pointed out that the capacity to exhibit rapid energy intake could be advantageous to deal with the lower temperatures or the irregular food availability of colder, temperate regions. Other authors referred to the lower metabolic rates of tropical species as possible consequences of non-migratory life strategies, notwithstanding the fact that the non-migratory nature of those strategies is not itself independent of climate (McNab, 2012). Finally, the capacity to migrate and evade from highly competitive environments in tropical regions as well as to avoid the difficult conditions of winter in temperate and polar regions, has been suggested has an important driver (Lindström, 1997). However, after Jetz *et al.* (2008) analysed how metabolism, migration, climate and phylogeny could be related, they concluded that the migratory capacity is not necessarily the explaining factor for high metabolic rates and that complex interactions exist between all these factors considered. These considerations allow us to propose the twelfth hypothesis of this study:

Hypothesis 12: bird species inhabiting tropical regions should exhibit lower assimilation and reserve mobilisation rates as well as lower somatic maintenance costs than bird species inhabiting temperate regions.

3.1.2.13 Conservation status

Most of the studies focused on existing patterns in the life history of birds and their possible association with the level of threat that bird species are facing and their current conservation status, have dealt with habitat availability (Pereira et al., 2004) climate change (Araújo et al., 2013, 2011; Langham et al., 2014) or other ecological aspects.

Studies relating the conservation status of bird species to their physiological and metabolic patterns have not been as common but recently the emergence of 'conservation physiology' (Cooke et al., 2013) as a research field has provided a background for a better integration of these two scopes. Detailed knowledge of avian metabolism may facilitate the establishment of indices of physiological stress and condition, allowing for better estimates on species persistence under different scenarios (e.g. land-use change, climate change and food-web disturbance) at all scales (Einoder, 2009; Ellis et al., 2012; Fort et al., 2011; Seebacher and Franklin, 2012).

Species that evolved in the absence of particular predation pressures (such as some bird species in insular environments where mammalian predators were absent) and exhibit slower growth rates may now be particularly vulnerable. Long incubation and nestling periods (up to fledging), and their inherent metabolic constraints may represent elements of vulnerability associated with higher conservation concerns. Taking these observations into consideration, the thirteenth and last hypothesis proposed for the present study is the following:

Hypothesis 13: bird species with a conservation status of higher concern should exhibit lower growth rates and longer incubation and nestling periods than unthreatened bird species.

3.1.3. General goal

The general goal of this study was to make use of the previously estimated DEB parameter sets (Teixeira et al., 2015) for a sample of forty species of birds and to investigate whether significant differences and patterns are observable, regarding DEB parameters and functions, between different categories grouping species within each indicated factor. These differences allowed us to test the set of hypotheses presented. Taking into account the expected distribution of values of each DEB parameter, according to their physical meaning and respective relationship with body size (i.e., whether they are considered to be intensive or design parameters), our aim was also to assess any observable deviation from these expectations – which may have ecological relevance – and identify which ecological factor(s) contribute to explain the additional scatter. Additionally, our aim was also to assess the relative contributions of body size and of each ecological factor to the variation of DEB parameters' values. Any deviations from these expectations should have ecological meaning and represent adaptations over the course of avian life history evolution. The association between particular ecological factors and the distribution of DEB parameter estimates, as well as the differences and patterns observed, allowed us to understand how metabolic diversity, expressed through the DEB parameters, implied properties and functions, may have constrained the phenotypic diversity observed in the life history of modern birds and the existing trade-offs between different life history traits. General conclusions relating our results to the present state of birds in the world were also discussed.

3.2 Methodology

3.2.1. Data used

The sample of bird species used in this study corresponds to the same sample presented by Teixeira *et al.* (2015), assembled in order to simultaneously cover the phylogenetic spectrum, at the taxonomic level of the Order, and the diversity of zoogeographic realms (Table 3.2). The set of life history traits published in the same study are presented in Table 3.3.

The DEB parameters' values adopted for this study correspond to those previously estimated in that study. These include primary DEB parameters (i.e., parameters connected to a single underlying process) at the reference temperature (T_{ref} = 293 K) (Table 3.4) and compound DEB parameters (i.e., parameters which are simple functions of two or more parameters) (Table 3.5). The compound DEB parameters considered, which can also be interpreted as implied properties of the theory, included: the zoom factor ($z = L_m / L_m^{ref} = \kappa \{\dot{p}_{Am}\} / [\dot{p}_M]$) (-), with $L_m^{ref} = 1$ cm, the maximum structural length ($L_m = [E_G]\, \dot{v} / [\dot{p}_M]\, g$) (cm) (which in this case will be equal to the zoom factor), the energy investment ratio ($g = [E_G]\, \dot{v} / \kappa \{\dot{p}_{Am}\}$) (-), the somatic maintenance rate coefficient ($\dot{k}_M = [\dot{p}_M]/[E_G]$) ($d^{-1}$), the maximum reserve capacity ($[E_m] = \{\dot{p}_{Am}\} / \dot{v}$) (J cm^{-3}) and the von Bertalanffy growth rate, ($\dot{r}_B = 1 / (3 / \dot{k}_M + 3\, f\, L_m / \dot{v})$) ($d^{-1}$).

Two other ecologically important traits were included, at the reference temperature, namely the dry mass-specific respiration ($-J_O / W_d$) (L g^{-1} h^{-1}) and the fasting capacity ($t_s = [E_m] / [\dot{p}_M]$) (d) (the amount of time during which the organism, once deprived of food, still has enough energy stored in reserve to cover the specific somatic maintenance costs) (Table 3.5).

The results published in the same study included additional properties, computed at the reference temperature, namely the maximum wet weight per ultimate structural volume (W_w^m / L_∞^3) (g cm^{-3}), the initial egg mass (i.e., the energy investment per offspring) (M_E^0) (C-mol), the specific allocation to reproduction per maximum structural volume as well ($\dot{p}_R^m / L_m^3 = (1 - \kappa)\, ([\dot{p}_M] / \kappa) - \dot{p}_J^p / L_m^3$) (J d^{-1} cm^{-3}) and the maturity maintenance at puberty per maximum structural volume ($\dot{p}_J^p / L_m^3 = \dot{k}_J\, E_H^p / L_m^3$) (J d^{-1} cm^{-3}) (Table 3.5). The input data used by Teixeira *et al.* (2015) (growth data obtained with full food availability, i.e., *ad libitum* (f = 1) and thermoregulatory capacities shared by all the species) allowed for the maximum structural volume (L_m^3) to be equal to the ultimate structural volume (L_∞^3).

All the rates obtained at the reference temperature were also converted to the corresponding values at each specific average adult body temperature (T_{am}) (Table 3.3), using a temperature correction factor (TC) obtained with the Arrhenius temperature (T_A = 1.5 × 10^4 K) through the following equation: $TC = \exp((T_A - T_{ref}) / (T_A - T_{am}))$ (Table 2.11).

The three core DEB parameters that express the cumulated energy invested into maturation up to the three most important maturity thresholds of the avian life cycle – birth (hatching) (E_H^b) (J), fledging (E_H^x) (J) and puberty (E_H^p) (J) are proportional to body size. In order to compare the species and their relative energetic investments in maturation up to each of these three thresholds we calculated the dry mass-specific maturity values at each threshold, i.e., the ratio between the amounts of energy invested in maturation, up to each moment, and the dry mass that the organism has already attained. For that purpose we used the volume-specific

structural mass of each species ($[M_V] = d_V^d/w_V$) (C-mol cm^{-3}) to compute the structural mass values at birth (hatching) ($M_V^b = [M_V] \times L_b^3$), at fledging ($M_V^x = [M_V] \times L_x^3$) and at puberty ($M_V^p = [M_V] \times L_p^3$) (C-mol), where L_b^3, L_x^3 and L_p^3 (cm^3) are the estimated structural volumes at each threshold. Then, the mass-specific maturity values at birth (hatching) ($\mu_H^b = E_H^b / M_V^b$), at fledging ($\mu_H^x = E_H^x / M_V^x$) and at puberty ($\mu_H^p = E_H^p / M_V^p$) (J mol^{-1}) were obtained (Table 3.7).

However, considering that these values correspond to energy that has in fact dissipated relative to a value of mass, we also calculated for the present study the 'altriciality index', i.e., the ratio between the cumulated energy invested in maturation up to puberty and the amount invested in maturation up to birth ($s^{pb}_H = E_H^p / E_H^b$), as it has been previously used to compare species of fish (Kooijman and Lika, 2014a).

The concept of altriciality is closely connected to the life history of birds. One of the most popular patterns in avian life history is related to growth and consists of a spectrum that includes species considered to be 'altricial' – the chicks hatch with their eyes closed and little or no down and are incapable of departing from the nest, this way requiring to be fed by the progenitors (or helpers) – which are in one end of the spectrum, and other species considered to be 'precocial' – the chicks hatch with their eyes opened, covered with down, and leave the nest within two days – which are at the opposite end of the spectrum. In between, several degrees of altriciality or precociality are considered to exist and the simplest way to group the species is within the 'semi-altricial' and 'semi-precocial' categories. The first category includes those birds that hatch already covered with down but are still incapable of departing from the nest and need to be fed by the progenitors. The second category includes those birds that hatch with eyes open, covered with down, and capable of leaving the nest soon after hatching (they can walk and often swim) but still use the nest and are fed by parents (Ehrlich et al., 1988).

The 'altriciality index' provides us with an indication of altriciality based on the ratio between puberty and birth, but considering the uncertainty regarding the exact moment when most species of birds reach sexual maturity (the age when they first reproduce may be an overestimate as puberty may be reached considerably before the first breeding season and behavioural constraints may delay the onset of reproduction) and the higher accuracy of average fledging times (the exact moment of fledging can actually be observed), we also calculated the same index using the ratio of energy investment in maturation up to fledging and birth ($s^{xb}_H = E_H^x / E_H^b$) (Table 3.7).

Finally, as alternative potential indicators of altriciality we calculated the ratios between the mass-specific maturity values at puberty and birth (μ_H^p / μ_H^b, -) and between the mass-specific maturity values at fledging and birth (μ_H^x / μ_H^b, -) (Table 3.7).

Table 3.2 – Collection of species selected for parameterization by Teixeira *et al.* (2015). The taxonomy and breeding range were obtained from the classification system adopted in the World Bird List of the International Ornithologists' Union (Gill and Donsker, 2012). Breeding range abbreviations are: Africa (AF) (whole continent); Antarctica (AN); Australasia (AU) (Indonesian islands east of Wallace's Line, New Guinea and its islands, Australia, New Zealand and its subantarctic islands, the Solomons, New Caledonia and Vanuatu); Eurasia (EU) (Europe, Asia from the Middle East through central Asia north of the Himalayas, Siberia and northern China to Japan); Latin America (LA) (Middle & South America); Indian Ocean (IO); Middle America (MA) (Mexico through Panama); North America (NA) (includes the Caribbean South America (SA); Oriental Region (OR) (South Asia from Pakistan to Taiwan, plus southeast Asia, the Philippines and Greater Sundas); Pacific Ocean (PO); Southern Ocean (SO); Tropical Ocean (TrO). The Zoogeographic realms where each species is resident and/or breeding were obtained from Holt et al. (2012) and the abbreviations are: Afrotropical (AFT); Australian (AUS); Madagascan (MAD); Nearctic (NEA); Neotropical (NEO); Oceanian (OCN); Oriental (ORI); Palearctic (PAL); Panamanian (PAN); Saharo-Arabian (SAH); Sino-Japanese (SIN).

Superorder	Order	Species	Common name	Breeding range	Zoogeographic realm (breeding)
Neognathae	Accipitriformes	*Aquila chrysaetos*	Golden Eagle	NA, MA, EU	AFT, NEA, ORI, PAL, SAH, SIN
Neognathae	Anseriformes	*Anas platyrhynchos*	Mallard	NA, EU	NEA, PAL, PAN, SAH, SIN
Neognathae	Apodiformes	*Apus apus*	Common Swift	EU	PAL, SAH, SIN
Neognathae	Bucerotiformes	*Bucorvus leadbeateri*	Southern Ground Hornbill	AF	AFT
Neognathae	Caprimulgiformes	*Podargus strigoides*	Tawny Frogmouth	AU	AUS
Neognathae	Cariamiformes	*Cariama cristata*	Red-legged Seriema	SA	NEO
Neognathae	Charadriiformes	*Larus argentatus*	European Herring Gull	EU	NEA, PAL, SAH
Neognathae	Ciconiiformes	*Ciconia ciconia*	White Stork	EU	PAL, SAH
Neognathae	Coliiformes	*Urocolius macrourus*	Blue-naped Mousebird	AF	AFT
Neognathae	Columbiformes	*Columba livia*	Rock Dove	Worldwide	AFT, AUS, NEA, OCN, ORI, PAL, PAN, SAH, SIN
Neognathae	Coraciiformes	*Todiramphus cinnamominus*	Micronesian Kingfisher	PO	OCN
Neognathae	Cuculiformes	*Cuculus canorus*	Common Cuckoo	EU	ORI, PAL, SAH, SIN
Neognathae	Eurypygiformes	*Rhynochetos jubatus*	Kagu	AU	OCN
Neognathae	Falconiformes	*Falco naumanni*	Lesser Kestrel	EU	PAL, SAH, SIN
Neognathae	Galliformes	*Gallus gallus*	Red Junglefowl	OR	AUS, OCN, ORI, SIN
Neognathae	Gaviiformes	*Gavia immer*	Great Northern Loon	NA, EU	NEA, PAL
Neognathae	Gruiformes	*Gallinula chloropus*	Common Moorhen	EU, AF, IO, OR, PO	AFT, MAD, NEA, NEO, ORI, PAN, SAH, SIN
Neognathae	Leptosomiformes	*Leptosomus discolor*	Cuckoo Roller	AF	MAD
Neognathae	Mesitornithiformes	*Mesitornis variegatus*	White-breasted Mesite	AF	MAD
Neognathae	Musophagiformes	*Tauraco erythrolophus*	Red-crested Turaco	AF	AFT
Neognathae	Opisthocoformes	*Opisthocomus hoazin*	Hoatzin	SA	NEO
Neognathae	Otidiformes	*Ardeotis kori*	Kori Bustard	AF	AFT
Neognathae	Passeriformes	*Parus major*	Great Tit	EU	ORI, PAL, SAH, SIN
Neognathae	Pelecaniformes	*Pelecanus onocrotalus*	Great White Pelican	EU	AFT, ORI, PAL, SAH
Neognathae	Phaethontiformes	*Phaethon rubricauda*	Red-tailed Tropicbird	TrO	AFT, AUS, MAD, OCN, ORI, SIN
Neognathae	Phoenicopteriformes	*Phoeniconaias minor*	Lesser Flamingo	AF, OR	AFT, ORI
Neognathae	Piciformes	*Ramphastos toco*	Toco Toucan	SA	NEO
Neognathae	Podicipediformes	*Podilymbus podiceps*	Pied-billed Grebe	NA, LA	NEA, NEO, PAN
Neognathae	Procellariiformes	*Diomedea exulans*	Wandering Albatross	SO	AFT, AUS, NEO
Neognathae	Psittaciformes	*Forpus passerinus*	Green-rumped Parrotlet	SA	NEO, PAN
Neognathae	Pteroclidiformes	*Pterocles alchata*	Pin-tailed Sandgrouse	EU	PAL, SAH
Neognathae	Sphenisciformes	*Pygoscelis adeliae*	Adelie Penguin	SO, AN	NEO, AUS
Neognathae	Strigiformes	*Tyto alba*	Western Barn Owl	NA, SA, AF, EU, OR	AFT, AUS, MAD, NEA, NEO, OCN, ORI, PAL, PAN, SAH
Neognathae	Suliformes	*Phalacrocorax auritus*	Double-crested Cormorant	NA, MA	NEA, PAN
Neognathae	Trogoniformes	*Euptilotis neoxenus*	Eared Quetzal	MA	NEA
Palaeognathae	Apterygiformes	*Apteryx mantelli*	North Island Brown Kiwi	AU	AUS
Palaeognathae	Casuariiformes	*Dromaius novaehollandiae*	Emu	AU	AUS
Palaeognathae	Rheiformes	*Rhea americana*	Greater Rhea	SA	NEO
Palaeognathae	Struthioniformes	*Struthio camelus*	Common Ostrich	AF	AFT
Palaeognathae	Tinamiformes	*Rhynchotus rufescens*	Red-winged Tinamou	SA	NEO

Table 3.3 – Sampled species and life history traits adopted from Teixeira *et al.* (2015): T_{ah} – average incubation temperature (K); T_{am} – average adult body temperature (K); a_h – incubation period (d); a_x – age at fledging (d); a_p – age at puberty (d); a_m –maximum life span (d); L_w – ultimate body length (from head to tail) (cm); W_w^h – hatchling wet weight (g); W_w^∞ – adult wet weight (g); $\dot{R}_\infty$ – maximum reproduction rate (# d^{-1}); W_w^∞ / W_d^∞ – ratio between wet weight and dry weight (-); d_V^d – specific density of dry structural mass (g cm^{-3}).

Species	T_{ah} (K)	T_{am} (K)	a_h (d)	a_x (d)	a_p (d)	a_m (d)	L_w (cm)	W_w^h (g)	W_w^∞ (g)	$\dot{R}_\infty$ (# d^{-1})	W_w^∞ / W_d^∞ (-)	d_V^d (g cm^{-3})
Aquila chrysaetos	309.7	311.5	44.0	67.5	1.46×10^3	1.75×10^4	81.5	105.0	4.23×10^3	5.48×10^{-3}	2.4	0.42
Anas platyrhynchos	309.7	314.2	27.5	55.0	210.0	1.06×10^4	57.5	32.4	1.06×10^3	3.01×10^{-2}	3.0	0.33
Apus apus	307.8	312.0	20.7	42.5	730.0	7.70×10^3	16.5	2.9	40.2	6.31×10^{-3}	2.3	0.43
Bucorvus leadbeateri	310.2	313.1	42.0	86.0	730.0	2.56×10^4	109.5	55.0	3.77×10^3	5.48×10^{-3}	2.4	0.42
Podargus strigoides	310.2	310.8	30.0	32.5	240.0	1.46×10^4	43.5	18.0	473.8	6.85×10^{-3}	2.3	0.43
Cariama cristata	310.2	312.0	27.5	30.0	240.0	1.17×10^4	90.0	61.5	2.75×10^3	5.48×10^{-3}	2.3	0.43
Larus argentatus	311.3	314.2	29.0	37.5	1.1×10^3	1.79×10^4	59.5	67.5	970.6	8.22×10^{-3}	2.8	0.36
Ciconia ciconia	308.5	312.5	32.0	61.0	1.46×10^3	1.42×10^4	112.5	72.5	3.30×10^3	1.33×10^{-2}	2.6	0.38
Urocolius macrourus	308.5	312.9	12.0	12.5	365.0	4.38×10^3	11.1	2.3	55.8	4.11×10^{-2}	2.6	0.38
Columba livia	310.9	313.6	18.0	36.0	140.0	1.28×10^4	32.5	15.2	300.00	1.64×10^{-2}	2.2	0.45
Todiramphus cinnamominus	310.8	312.6	23.0	33.0	304.8	4.75×10^3	22.0	5.8	63.2	1.10×10^{-2}	2.9	0.34
Cuculus canorus	309.3	313.0	11.7	19.0	365.0	4.71×10^3	33.0	2.6	115.0	2.52×10^{-2}	2.8	0.36
Rhynochetos jubatus	310.5	310.8	35.0	109.0	730.0	1.1×10^4	60.0	67.5	900.0	2.74×10^{-3}	2.3	0.43
Falco naumanni	308.3	312.0	28.5	28.0	365.0	3.98×10^3	30.5	10.3	151.3	1.10×10^{-2}	2.3	0.43
Gallus gallus	310.5	314.0	21.0	7.0	174.3	9.13×10^3	57.0	26.7	959.3	1.64×10^{-2}	2.6	0.38
Gavia immer	310.5	312.0	24.5	73.5	730.0	8.80×10^3	80.0	79.6	4.04×10^3	5.48×10^{-3}	2.5	0.40
Gallinula chloropus	308.0	312.6	21.5	45.0	365.0	6.79×10^3	33.5	13.9	320.0	3.84×10^{-2}	3.2	0.31
Leptosomus discolor	310.8	312.6	20.0	30.0	365.0	1.01×10^4	45.0	3.0	225.0	1.10×10^{-2}	2.9	0.34
Mesitornis variegatus	310.9	313.6	24.3	-	365.0	4.82×10^3	31.0	5.0	107.0	5.48×10^{-3}	2.2	0.45
Tauraco erythrolophus	310.2	312.0	24.0	31.5	240.0	9.86×10^3	48.5	16.0	267.5	5.48×10^{-3}	2.5	0.40
Opisthocomus hoazin	310.5	312.0	32.0	17.5	365.0	1.1×10^4	66.0	20.9	750.0	6.85×10^{-3}	2.8	0.36
Ardeotis kori	310.5	313.3	23.0	31.5	730.0	1.17×10^4	116.5	99.7	9.38×10^3	4.16×10^{-3}	2.8	0.36
Parus major	308.4	314.0	13.9	19.0	365.0	5.48×10^3	14.0	1.3	18.0	4.59×10^{-2}	3.0	0.33
Pelecanus onocrotalus	310.6	312.0	32.5	80.0	1.1×10^3	1.86×10^4	157.5	106.2	8.90×10^3	5.48×10^{-3}	2.5	0.40
Phaethon rubricauda	308.0	311.5	45.0	79.0	274.0	1.19×10^4	79.5	54.0	717.5	2.74×10^{-3}	2.8	0.36
Phoeniconaias minor	310.2	312.5	28.0	77.5	730.0	1.83×10^4	85.0	85.5	1.73×10^3	2.74×10^{-3}	2.8	0.36
Ramphastos toco	310.2	311.9	17.5	47.5	1.1×10^3	9.49×10^3	61.0	16.0	665.6	8.22×10^{-3}	2.9	0.34
Podilymbus podiceps	309.5	312.6	25.0	43.5	365.0	4.98×10^3	34.5	14.9	440.0	1.64×10^{-2}	2.8	0.36
Diomedea exulans	308.8	312.6	79.5	255.0	2.2×10^3	2.19×10^4	122.5	379.0	7.86×10^3	1.37×10^{-3}	2.0	0.50
Forpus passerinus	307.5	311.8	21.0	35.0	365.0	9.13×10^3	12.0	1.9	25.0	3.84×10^{-2}	3.0	0.33
Pterocles alchata	311.3	314.4	22.0	30.0	365.0	9.65×10^3	35.0	13.8	309.8	6.85×10^{-3}	2.2	0.45
Pygoscelis adeliae	308.8	311.2	35.2	28.0	1.1×10^3	5.84×10^3	69.9	81.0	5.00×10^3	5.48×10^{-3}	2.0	0.50
Tyto alba	307.0	312.0	33.0	52.5	365	7.78×10^3	34.0	15.0	334.46	3.29×10^{-2}	2.4	0.42
Phalacrocorax auritus	310.2	313.7	26.5	24.5	730.0	8.21×10^3	82.5	34.1	1.90×10^3	1.10×10^{-2}	2.9	0.34
Euptilotis neoxenus	310.8	312.6	22.0	30.0	1.83×10^3	9.13×10^3	34.5	14.5	122.50	5.48×10^{-3}	2.9	0.34
Apteryx mantelli	304.0	311.2	82.5	25.0	915.0	1.83×10^4	79.8	239.3	2.35×10^3	1.64×10^{-2}	2.6	0.38
Dromaius novaehollandiae	309.0	311.0	53.0	4.5	540.0	1.46×10^4	134.0	420.0	4.25×10^4	2.74×10^{-2}	2.6	0.38
Rhea americana	309.5	312.7	36.0	150.0	426.0	7.30×10^3	129.0	358.6	2.25×10^4	2.05×10^{-2}	2.6	0.38
Struthio camelus	307.6	311.6	40.5	135.0	1.1×10^3	1.83×10^4	212.5	816.0	12.03×10^4	1.64×10^{-2}	2.3	0.43
Rhynchotus rufescens	309.0	312.6	20.0	7.0	210.0	5.48×10^3	40.8	35.5	868.75	1.10×10^{-2}	2.6	0.38

Table 3.4 – Estimated values for the main primary (core and auxiliary) DEB parameters at the reference temperature (T_{ref} = 293 K). The parameter abbreviations and their corresponding names are the following: δ_M – shape coefficient (-); $\{\dot{p}_{Am}\}$ – maximum specific assimilation rate (J d^{-1} cm^{-2}); κ – allocation fraction to soma (-); $\dot{v}$ – energy conductance (cm d^{-1}); $[\dot{p}_M]$ – volume-specific somatic maintenance rate (J d^{-1} cm^{-3}); E_H^b – maturity at birth (hatching) (J); E_H^x – maturity at fledging (J); E_H^p – maturity at puberty (J); $\dot{k}_J$ – maturity maintenance rate coefficient (d^{-1}); $[E_G]$ – specific cost for structure (J cm^{-3}); $\ddot{h}_a$ – Weibull ageing acceleration (d^{-2}). Statistical abbreviations are as follow: $\bar{x}$ – mean; SE – standard error; $\tilde{x}$ – median; Q_1 – lower quartile; Q_3 – upper quartile; c_v – coefficient of variation.

Species	δ_M (-)	$\{\dot{p}_{Am}\}$ (J d^{-1} cm^{-2})	κ (-)	$\dot{v}$ (cm d^{-1})	$[\dot{p}_M]$ (J d^{-1} cm^{-3})	E_H^b (J)	E_H^x (J)	E_H^p (J)	$\dot{k}_J$ (d^{-1})	$[E_G]$ (J cm^{-3})	$\ddot{h}_a$ (d^{-2})
Aquila chrysaetos	0.17	1.01×10^{3}	0.998	0.19	72.24	1.57×10^{3}	2.41×10^{5}	9.28×10^{6}	1.41×10^{-8}	1.10×10^{4}	7.47×10^{-33}
Anas platyrhynchos	0.16	3.40×10^{2}	0.989	9.36×10^{-2}	37.52	2.58×10^{3}	2.45×10^{5}	1.63×10^{6}	1.14×10^{-7}	8.59×10^{3}	3.50×10^{-26}
Apus apus	0.20	4.40×10^{2}	0.998	0.35	133.32	70.82	7.29×10^{3}	8.26×10^{4}	3.21×10^{-6}	1.12×10^{4}	9.77×10^{-90}
Bucorvus leadbeateri	0.11	6.33×10^{2}	0.999	6.11×10^{-2}	51.81	553.47	1.32×10^{5}	2.79×10^{5}	6.48×10^{-6}	1.09×10^{4}	1.93×10^{-26}
Podargus strigoides	0.16	7.20×10^{2}	0.998	0.25	100.30	271.24	1.77×10^{4}	2.15×10^{5}	3.11×10^{-5}	1.12×10^{4}	1.50×10^{-51}
Cariama cristata	0.14	6.25×10^{2}	0.998	0.14	50.58	1.08×10^{3}	2.87×10^{4}	7.73×10^{5}	4.45×10^{-6}	1.12×10^{4}	1.73×10^{-23}
Larus argentatus	0.14	6.35×10^{2}	0.996	0.11	74.54	2.23×10^{3}	1.27×10^{5}	6.89×10^{7}	2.37×10^{-9}	9.32×10^{3}	1.40×10^{-43}
Ciconia ciconia	0.11	1.44×10^{3}	0.998	0.24	115.10	1.07×10^{3}	4.47×10^{5}	7.22×10^{7}	1.85×10^{-7}	9.87×10^{3}	1.30×10^{-39}
Urocolius macrourus	0.32	3.55×10^{2}	0.991	0.20	97.76	199.33	4.55×10^{3}	1.11×10^{5}	9.66×10^{-7}	9.82×10^{3}	2.86×10^{-37}
Columba livia	0.19	4.90×10^{2}	0.994	0.18	78.64	1.03×10^{3}	6.43×10^{4}	3.95×10^{5}	1.17×10^{-7}	1.18×10^{4}	5.85×10^{-57}
Todiramphus cinnamominus	0.17	3.01×10^{2}	0.993	0.17	80.30	352.36	1.45×10^{4}	8.34×10^{4}	3.79×10^{-5}	8.86×10^{3}	3.36×10^{-33}
Cuculus canorus	0.14	6.05×10^{2}	0.998	0.31	133.27	46.50	6.37×10^{3}	4.99×10^{4}	2.59×10^{-6}	9.37×10^{3}	3.78×10^{-46}
Rhynochetos jubatus	0.15	5.52×10^{2}	0.991	0.15	60.63	5.63×10^{3}	4.53×10^{5}	1.22×10^{6}	2.48×10^{-4}	1.11×10^{4}	9.13×10^{-26}
Falco naumanni	0.16	9.51×10^{2}	0.997	0.43	189.99	314.03	2.83×10^{4}	4.00×10^{5}	3.29×10^{-7}	1.14×10^{4}	5.18×10^{-43}
Gallus gallus	0.15	2.37×10^{2}	0.963	4.41×10^{-2}	27.13	7.37×10^{3}	1.83×10^{4}	8.35×10^{5}	5.37×10^{-4}	9.93×10^{3}	6.48×10^{-18}
Gavia immer	0.17	7.75×10^{2}	0.998	0.16	55.88	990.75	1.79×10^{5}	1.38×10^{6}	7.43×10^{-8}	1.04×10^{4}	6.01×10^{-21}
Gallinula chloropus	0.18	3.30×10^{2}	0.983	0.10	53.74	1.64×10^{3}	1.11×10^{5}	9.61×10^{5}	1.36×10^{-6}	8.06×10^{3}	7.22×10^{-23}
Leptosomus discolor	0.11	83.56	0.993	1.16×10^{-2}	16.96	115.59	8.93×10^{2}	6.66×10^{4}	6.59×10^{-7}	8.89×10^{3}	8.95×10^{-15}
Mesitornis variegatus	0.13	1.15×10^{2}	0.993	2.39×10^{-2}	27.43	323.01	-	1.08×10^{5}	1.12×10^{-7}	1.18×10^{4}	6.41×10^{-15}
Tauraco erythrolophus	0.12	2.12×10^{2}	0.994	6.14×10^{-2}	36.28	874.92	9.40×10^{3}	1.80×10^{5}	3.99×10^{-7}	1.04×10^{4}	3.57×10^{-21}
Opisthocomus hoazin	0.12	3.25×10^{2}	0.997	9.14×10^{-2}	40.23	571.03	5.15×10^{3}	4.85×10^{5}	1.96×10^{-7}	9.36×10^{3}	4.87×10^{-23}

Ardeotis kori	0.14	3.34×10^{2}	0.998	3.10×10^{-2}	20.84	980.65	1.07×10^{4}	2.43×10^{6}	4.56×10^{-8}	9.40×10^{3}	4.68×10^{-15}
Parus major	0.18	3.51×10^{2}	0.991	0.27	139.73	98.44	7.52×10^{3}	2.05×10^{5}	7.04×10^{-7}	8.59×10^{3}	1.28×10^{-87}
Pelecanus onocrotalus	0.11	6.24×10^{2}	0.998	9.55×10^{-2}	35.93	1.24×10^{3}	1.62×10^{5}	3.15×10^{6}	3.67×10^{-8}	1.04×10^{4}	1.46×10^{-21}
Phaethon rubricauda	0.11	6.63×10^{2}	0.998	0.21	78.06	745.63	9.15×10^{4}	4.89×10^{5}	3.21×10^{-7}	9.39×10^{3}	1.97×10^{-37}
Phoeniconaias minor	0.12	5.90×10^{2}	0.998	0.16	55.50	1.17×10^{3}	1.31×10^{5}	2.24×10^{6}	3.35×10^{-6}	9.35×10^{3}	5.87×10^{-40}
Ramphastos toco	0.12	5.33×10^{2}	0.998	0.11	71.76	218.49	2.80×10^{4}	1.37×10^{6}	6.50×10^{-8}	8.78×10^{3}	7.76×10^{-24}
Podilymbus podiceps	0.20	3.57×10^{2}	0.994	0.13	51.25	777.15	4.99×10^{4}	5.64×10^{5}	3.01×10^{-6}	9.35×10^{3}	1.31×10^{-20}
Diomedea exulans	0.12	1.00×10^{3}	0.998	5.99×10^{-2}	67.75	4.84×10^{3}	1.66×10^{6}	1.83×10^{7}	1.63×10^{-8}	1.30×10^{4}	2.47×10^{-21}
Forpus passerinus	0.23	2.75×10^{2}	0.984	0.20	97.71	255.42	1.65×10^{4}	7.65×10^{4}	2.39×10^{-6}	8.59×10^{3}	6.32×10^{-73}
Pterocles alchata	0.18	2.64×10^{2}	0.996	8.29×10^{-2}	42.41	571.89	1.30×10^{4}	3.15×10^{5}	6.05×10^{-7}	1.17×10^{4}	4.84×10^{-29}
Pygoscelis adeliae	0.22	1.43×10^{3}	0.999	0.28	94.41	842.81	4.75×10^{4}	5.24×10^{6}	4.71×10^{-8}	1.31×10^{4}	9.06×10^{-20}
Tyto alba	0.17	4.30×10^{2}	0.980	6.06×10^{-2}	72.99	2.52×10^{3}	1.51×10^{5}	1.62×10^{6}	3.00×10^{-7}	1.09×10^{4}	6.08×10^{-19}
Phalacrocorax auritus	0.13	7.44×10^{2}	0.998	0.17	69.74	348.93	2.95×10^{4}	2.69×10^{6}	8.86×10^{-9}	8.89×10^{3}	5.32×10^{-27}
Euptilotis neoxenus	0.13	3.54×10^{2}	0.995	0.13	78.67	587.37	1.49×10^{4}	9.17×10^{5}	2.21×10^{-7}	8.77×10^{3}	1.31×10^{-37}
Apteryx mantelli	0.15	1.27×10^{2}	0.791	5.02×10^{-2}	8.20	5.77×10^{5}	1.01×10^{6}	4.47×10^{7}	2.54×10^{-5}	9.96×10^{3}	3.17×10^{-18}
Dromaius novaehollandiae	0.18	7.24×10^{2}	0.985	3.04×10^{-2}	29.06	2.48×10^{4}	3.55×10^{4}	3.30×10^{7}	1.61×10^{-6}	9.85×10^{3}	4.29×10^{-14}
Rhea americana	0.19	2.63×10^{2}	0.978	4.13×10^{-2}	10.55	5.46×10^{4}	2.63×10^{6}	1.61×10^{7}	2.39×10^{-6}	9.94×10^{3}	1.34×10^{-13}
Struthio camelus	0.17	9.07×10^{2}	0.993	4.99×10^{-2}	25.18	2.82×10^{4}	3.36×10^{6}	1.35×10^{8}	1.93×10^{-8}	1.12×10^{4}	5.57×10^{-15}
Rhynchotus rufescens	0.19	2.23×10^{2}	0.986	3.97×10^{-2}	28.63	3.95×10^{3}	7.92×10^{3}	5.86×10^{5}	5.57×10^{-8}	9.85×10^{3}	1.42×10^{-14}
$\bar{x}$	0.16	5.34×10^{2}	0.988	0.14	65.30	1.83×10^{4}	2.97×10^{5}	1.07×10^{7}	2.29×10^{-5}	1.01×10^{4}	5.43×10^{-15}
SE	6.59×10^{-3}	50.88	5.19×10^{-3}	1.55×10^{-2}	6.22	1.44×10^{4}	1.13×10^{5}	4.19×10^{6}	1.46×10^{-5}	1.93×10^{2}	3.50×10^{-15}
$\tilde{x}$	0.16	4.65×10^{2}	0.995	0.12	58.26	9.28×10^{2}	3.55×10^{4}	8.76×10^{5}	3.64×10^{-7}	9.90×10^{3}	3.93×10^{-24}
Q_1	0.13	3.13×10^{2}	0.991	6.03×10^{-2}	36.11	3.36×10^{2}	1.30×10^{4}	2.47×10^{5}	6.97×10^{-8}	9.34×10^{3}	6.62×10^{-38}
Q_3	0.18	6.91×10^{2}	0.998	0.20	79.48	2.38×10^{3}	1.62×10^{5}	2.92×10^{6}	2.80×10^{-6}	1.12×10^{4}	3.49×10^{-19}
c_v	0.26	0.60	0.03	0.70	0.60	4.98	2.39	2.47	4.03	0.12	4.08

Table 3.5 – Estimated values for the main compound DEB parameters and additional properties at the reference temperature (T_{ref} = 293 K). The parameter abbreviations and their corresponding names are the following: z – zoom factor (-); g – energy investment ratio (-); $\dot{k}_M$ – somatic maintenance rate coefficient (d^{-1}); $[E_m]$ – maximum reserve capacity (J cm^{-3}); $\dot{r}_B$ – von Bertalanffy growth rate (d^{-1}); $-J_O / W_d$ – dry mass-specific respiration (L g^{-1} h^{-1}); t_s – fasting capacity (d); W_w^m / L_∞^3 – maximum wet weight per ultimate structural volume (g cm^{-3}); M_E^0 – initial egg mass (C-mol); $\dot{p}_R^m / L_m^3$ – specific allocation to reproduction per maximum structural volume (J d^{-1} cm^{-3}); $\dot{p}_J^p / L_m^3$ – maturity maintenance at puberty per maximum structural volume (J d^{-1} cm^{-3}). Statistical abbreviations are as follow: $\bar{x}$ – mean; SE – standard error; $\tilde{x}$ – median; Q_1 – lower quartile; Q_3 – upper quartile; c_v – coefficient of variation.

Species	z (-)	g (-)	$\dot{k}_M$ (d^{-1})	$[E_m]$ (J cm^{-3})	$\dot{r}_B$ (d^{-1})	$-J_O / W_d$ (L g^{-1} h^{-1})	t_s (d)	W_w^m / L_∞^3 (g cm^{-3})	M_E^0 (C-mol)	$\dot{p}_R^m / L_m^3$ (J d^{-1} cm^{-3})	$\dot{p}_J^p / L_m^3$ (J d^{-1} cm^{-3})
Aquila chrysaetos	14.01	2.11	6.58×10^{-3}	5.21×10^{3}	1.49×10^{-3}	2.29×10^{-4}	2.00×10^{2}	1.54	2.29	0.13	4.75×10^{-5}
Anas platyrhynchos	8.96	2.39	4.37×10^{-3}	3.63×10^{3}	1.03×10^{-3}	1.58×10^{-4}	28.61	1.48	0.56	0.43	2.57×10^{-4}
Apus apus	3.29	8.96	1.19×10^{-2}	1.25×10^{3}	3.58×10^{-3}	5.58×10^{-4}	91.19	1.13	6.39×10^{-2}	0.29	7.43×10^{-3}
Bucorvus leadbeateri	12.21	1.05	4.75×10^{-3}	1.04×10^{4}	8.13×10^{-4}	1.20×10^{-4}	75.12	2.07	1.17	7.65×10^{-2}	9.95×10^{-4}
Podargus strigoides	7.16	3.92	8.94×10^{-3}	2.87×10^{3}	2.37×10^{-3}	3.68×10^{-4}	51.75	1.29	0.31	0.18	1.82×10^{-2}
Cariama cristata	12.33	2.43	4.52×10^{-3}	4.61×10^{3}	1.07×10^{-3}	1.64×10^{-4}	17.83	1.47	1.33	9.95×10^{-2}	1.83×10^{-3}
Larus argentatus	8.48	1.67	7.99×10^{-3}	5.60×10^{3}	1.67×10^{-3}	2.53×10^{-4}	34.52	1.68	1.33	0.33	2.68×10^{-4}
Ciconia ciconia	12.52	1.66	1.17×10^{-2}	5.96×10^{3}	2.43×10^{-3}	3.65×10^{-4}	21.84	1.68	1.42	0.23	6.82×10^{-3}
Urocolius macrourus	3.60	5.69	9.95×10^{-3}	1.74×10^{3}	2.82×10^{-3}	4.38×10^{-4}	14.65	1.20	4.56×10^{-2}	0.90	2.31×10^{-3}
Columba livia	6.19	4.36	6.69×10^{-3}	2.71×10^{3}	1.81×10^{-3}	2.83×10^{-4}	59.05	1.26	0.36	0.50	1.95×10^{-4}
Todiramphus cinnamominus	3.72	5.09	9.06×10^{-3}	1.75×10^{3}	2.52×10^{-3}	3.92×10^{-4}	11.54	1.22	0.10	0.52	6.11×10^{-2}
Cuculus canorus	4.53	4.81	1.42×10^{-2}	1.95×10^{3}	3.92×10^{-3}	6.11×10^{-4}	1.98×10^{2}	1.24	4.74×10^{-2}	0.28	1.39×10^{-3}
Rhynochetos jubatus	9.02	3.14	5.44×10^{-3}	3.58×10^{3}	1.38×10^{-3}	2.13×10^{-4}	85.53	1.36	1.40	0.16	0.41
Falco naumanni	4.99	5.21	1.67×10^{-2}	2.19×10^{3}	4.66×10^{-3}	7.22×10^{-4}	60.20	1.22	0.24	0.53	1.06×10^{-3}
Gallus gallus	8.41	1.92	2.73×10^{-3}	5.37×10^{3}	5.99×10^{-4}	9.45×10^{-5}	4.24×10^{2}	1.61	0.54	0.28	0.75
Gavia immer	13.85	2.18	5.38×10^{-3}	4.78×10^{3}	1.23×10^{-3}	1.86×10^{-4}	1.76×10^{2}	1.52	1.63	8.59×10^{-2}	3.85×10^{-5}
Gallinula chloropus	6.04	2.53	6.67×10^{-3}	3.24×10^{3}	1.59×10^{-3}	2.42×10^{-4}	94.97	1.45	0.23	0.93	5.91×10^{-3}
Leptosomus discolor	4.89	1.25	1.91×10^{-3}	7.19×10^{3}	3.53×10^{-4}	5.25×10^{-5}	88.58	1.92	5.20×10^{-2}	0.11	3.74×10^{-4}
Mesitornis variegatus	4.18	2.45	2.33×10^{-3}	4.83×10^{3}	5.52×10^{-4}	8.61×10^{-5}	5.17×10^{2}	1.46	0.12	0.18	1.65×10^{-4}
Tauraco erythrolophus	5.80	3.04	3.48×10^{-3}	3.45×10^{3}	8.74×10^{-4}	1.33×10^{-4}	9.36	1.37	0.32	0.23	3.68×10^{-4}

Opisthocomus hoazin	8.06	2.64	4.30×10^{-3}	3.56×10^{3}	1.04×10^{-3}	1.59×10^{-4}	1.82×10^{2}	1.43	0.41	0.14	1.81×10^{-4}
Ardeotis kori	15.97	0.87	2.22×10^{-3}	1.08×10^{4}	3.45×10^{-4}	5.12×10^{-5}	40.03	2.30	1.80	3.90×10^{-2}	2.71×10^{-5}
Parus major	2.49	6.63	1.63×10^{-2}	1.31×10^{3}	4.71×10^{-3}	7.40×10^{-4}	66.02	1.17	2.24×10^{-2}	1.27	9.40×10^{-3}
Pelecanus onocrotalus	17.33	1.60	3.44×10^{-3}	6.53×10^{3}	7.06×10^{-4}	1.06×10^{-4}	69.17	1.71	2.14	5.78×10^{-2}	2.22×10^{-5}
Phaethon rubricauda	8.48	3.01	8.31×10^{-3}	3.13×10^{3}	2.08×10^{-3}	3.19×10^{-4}	52.89	1.38	1.04	0.13	2.57×10^{-4}
Phoeniconaias minor	10.62	2.56	5.94×10^{-3}	3.66×10^{3}	1.42×10^{-3}	2.17×10^{-4}	2.46×10^{2}	1.44	1.63	8.88×10^{-2}	6.29×10^{-3}
Ramphastos toco	7.41	1.77	8.17×10^{-3}	4.96×10^{3}	1.74×10^{-3}	2.63×10^{-4}	13.85	1.63	0.28	0.15	2.19×10^{-4}
Podilymbus podiceps	6.92	3.47	5.48×10^{-3}	2.71×10^{3}	1.42×10^{-3}	2.18×10^{-4}	74.93	1.33	0.28	0.32	5.13×10^{-3}
Diomedea exulans	14.75	0.78	5.20×10^{-3}	1.67×10^{4}	7.61×10^{-4}	1.13×10^{-4}	54.38	2.45	10.39	0.10	9.27×10^{-5}
Forpus passerinus	2.77	6.45	1.14×10^{-2}	1.35×10^{3}	3.28×10^{-3}	5.11×10^{-4}	97.22	1.17	3.31×10^{-2}	1.57	8.58×10^{-3}
Pterocles alchata	6.19	3.71	3.62×10^{-3}	3.18×10^{3}	9.49×10^{-4}	1.47×10^{-4}	63.80	1.31	0.33	0.17	8.05×10^{-4}
Pygoscelis adeliae	15.12	2.54	7.23×10^{-3}	5.13×10^{3}	1.73×10^{-3}	2.65×10^{-4}	35.85	1.45	2.05	9.44×10^{-2}	7.15×10^{-5}
Tyto alba	5.78	1.56	6.72×10^{-3}	7.10×10^{3}	1.37×10^{-3}	2.04×10^{-4}	3.08×10^{2}	1.73	0.34	1.49	2.52×10^{-3}
Phalacrocorax auritus	10.66	2.00	7.85×10^{-3}	4.45×10^{3}	1.74×10^{-3}	2.66×10^{-4}	8.19×10^{2}	1.57	0.59	0.11	1.97×10^{-5}
Euptilotis neoxenus	4.48	3.13	8.97×10^{-3}	2.82×10^{3}	2.26×10^{-3}	3.47×10^{-4}	6.04×10^{2}	1.36	0.27	0.39	2.25×10^{-3}
Apteryx mantelli	12.22	4.99	8.23×10^{-4}	2.52×10^{3}	2.29×10^{-4}	3.52×10^{-5}	7.22×10^{2}	1.29	5.89	1.55	0.62
Dromaius novaehollandiae	24.54	0.42	2.95×10^{-3}	2.38×10^{4}	2.91×10^{-4}	4.15×10^{-5}	1.96×10^{2}	3.72	7.89	0.44	3.59×10^{-3}
Rhea americana	24.37	1.60	1.06×10^{-3}	6.37×10^{3}	2.17×10^{-4}	3.18×10^{-5}	2.00×10^{2}	1.73	7.02	0.23	2.65×10^{-3}
Struthio camelus	35.78	0.62	2.25×10^{-3}	1.82×10^{4}	2.87×10^{-4}	4.23×10^{-5}	28.61	2.84	17.24	0.17	5.67×10^{-5}
Rhynchotus rufescens	7.68	1.78	2.91×10^{-3}	5.62×10^{3}	6.20×10^{-4}	9.28×10^{-5}	91.19	1.64	0.73	0.41	7.19×10^{-5}
$\bar{x}$	9.90	2.95	6.51×10^{-3}	5.40×10^{3}	1.60×10^{-3}	2.46×10^{-4}	152.05	1.60	1.85	0.38	4.85×10^{-2}
SE	1.07	0.29	6.23×10^{-4}	7.42×10^{-2}	1.85×10^{-4}	2.89×10^{-5}	31.19	7.86×10^{-2}	0.54	6.64×10^{-2}	2.58×10^{-2}
$\tilde{x}$	8.24	2.49	5.71×10^{-3}	4.06×10^{3}	1.40×10^{-3}	2.15×10^{-4}	73.54	1.46	0.55	0.23	1.03×10^{-3}
Q_1	5.39	1.67	3.46×10^{-3}	2.77×10^{3}	7.33×10^{-4}	1.10×10^{-4}	37.94	1.30	0.25	0.12	1.73×10^{-4}
Q_3	12.42	3.81	8.63×10^{-3}	5.79×10^{3}	2.17×10^{-3}	3.33×10^{-4}	188.98	1.68	1.63	0.43	6.10×10^{-3}
c_v	0.68	0.63	0.60	0.87	0.73	0.74	1.3	0.31	1.84	1.09	3.36

Table 3.6 – Estimated values for selected primary and compound DEB parameters at each specific average adult body temperature (T_{am}). The parameter abbreviations and their corresponding names are the following: $\{\dot{p}_{Am}^{T}\}$ – maximum surface-specific assimilation rate (J d^{-1} cm^{-2}); $\dot{v}^{T}$ – energy conductance (cm d^{-1}); $[\dot{p}_{M}^{T}]$ – volume-specific somatic maintenance rate (J d^{-1} cm^{-3}); $\dot{k}_{J}^{T}$ – maturity maintenance rate coefficient (d^{-1}); $\dot{k}_{M}^{T}$ – somatic maintenance rate coefficient (d^{-1}); $\dot{r}_{B}^{T}$ – von Bertalanffy growth rate (d^{-1}); -J_{O}^{T} / W_{d} – dry mass-specific respiration (L g^{-1} h^{-1}); t_{s}^{T} – fasting capacity (d). Statistical abbreviations are as follow: $\bar{x}$ – mean; SE – standard error; $\tilde{x}$ – median; Q_1 – lower quartile; Q_3 – upper quartile; c_v – coefficient of variation.

Species	$\{\dot{p}_{Am}^{T}\}$ (J d^{-1} cm^{-2})	$\dot{v}^{T}$ (cm d^{-1})	$[\dot{p}_{M}^{T}]$ (J d^{-1} cm^{-3})	$\dot{k}_{J}^{T}$ (d^{-1})	$\dot{k}_{M}^{T}$ (d^{-1})	$\dot{r}_{B}^{T}$ (d^{-1})	-J_{O}^{T} / W_{d} (L g^{-1} h^{-1})	t_{s}^{T} (d)
Aquila chrysaetos	2.13 × 10^{4}	4.08	1.52 × 10^{3}	2.95 × 10^{-7}	0.14	3.12 × 10^{-2}	4.80 × 10^{-3}	3.44
Anas platyrhynchos	1.08 × 10^{4}	2.96	1.19 × 10^{3}	3.59 × 10^{-6}	0.14	3.25 × 10^{-2}	5.00 × 10^{-3}	3.06
Apus apus	9.94 × 10^{3}	7.96	3.01 × 10^{3}	7.26 × 10^{-5}	0.27	8.09 × 10^{-2}	1.26 × 10^{-2}	0.41
Bucorvus leadbeateri	1.69 × 10^{4}	1.63	1.39 × 10^{3}	1.74 × 10^{-4}	0.13	2.17 × 10^{-2}	3.20 × 10^{-3}	7.48
Podargus strigoides	1.35 × 10^{4}	4.71	1.88 × 10^{3}	5.84 × 10^{-4}	0.17	4.46 × 10^{-2}	6.90 × 10^{-3}	1.52
Cariama cristata	1.41 × 10^{4}	3.06	1.14 × 10^{3}	1.01 × 10^{-4}	0.10	2.41 × 10^{-2}	3.70 × 10^{-3}	4.04
Larus argentatus	2.01 × 10^{4}	3.59	2.36 × 10^{3}	7.50 × 10^{-8}	0.25	5.28 × 10^{-2}	8.00 × 10^{-3}	2.37
Ciconia ciconia	3.52 × 10^{4}	5.91	2.81 × 10^{3}	4.52 × 10^{-6}	0.28	5.92 × 10^{-2}	8.90 × 10^{-3}	2.12
Urocolius macrourus	9.16 × 10^{3}	5.26	2.52 × 10^{3}	2.49 × 10^{-5}	0.26	7.29 × 10^{-2}	1.13 × 10^{-2}	0.69
Columba livia	1.42 × 10^{4}	5.24	2.28 × 10^{3}	3.40 × 10^{-6}	0.19	5.26 × 10^{-2}	8.20 × 10^{-3}	1.19
Todiramphus cinnamominus	7.46 × 10^{3}	4.26	1.99 × 10^{3}	9.38 × 10^{-4}	0.22	6.25 × 10^{-2}	9.70 × 10^{-3}	0.88
Cuculus canorus	1.59 × 10^{4}	8.17	3.51 × 10^{3}	6.82 × 10^{-5}	0.38	0.10	1.61 × 10^{-2}	0.56
Rhynochetos jubatus	1.04 × 10^{4}	2.89	1.14 × 10^{3}	4.66 × 10^{-3}	0.10	2.58 × 10^{-2}	4.00 × 10^{-3}	3.15
Falco naumanni	2.15 × 10^{4}	9.80	4.29 × 10^{3}	7.44 × 10^{-6}	0.38	0.11	1.63 × 10^{-2}	0.51
Gallus gallus	7.27 × 10^{3}	1.35	8.32 × 10^{2}	1.65 × 10^{-2}	8.38 × 10^{-2}	1.84 × 10^{-2}	2.90 × 10^{-3}	6.45
Gavia immer	1.75 × 10^{4}	3.67	1.26 × 10^{3}	1.68 × 10^{-6}	0.12	2.77 × 10^{-2}	4.20 × 10^{-3}	3.79
Gallinula chloropus	8.18 × 10^{3}	2.53	1.33 × 10^{3}	3.36 × 10^{-5}	0.17	3.95 × 10^{-2}	6.00 × 10^{-3}	2.43
Leptosomus discolor	2.07 × 10^{3}	0.29	4.20 × 10^{2}	1.63 × 10^{-5}	4.73 × 10^{-2}	8.70 × 10^{-3}	1.30 × 10^{-3}	17.11
Mesitornis variegatus	3.35 × 10^{3}	0.69	7.96 × 10^{2}	3.25 × 10^{-6}	6.77 × 10^{-2}	1.60 × 10^{-2}	2.50 × 10^{-3}	6.07
Tauraco erythrolophus	4.78 × 10^{3}	1.39	8.20 × 10^{2}	9.01 × 10^{-6}	7.87 × 10^{-2}	1.97 × 10^{-2}	3.00 × 10^{-3}	4.20

Opisthocomus hoazin	7.35×10^{3}	2.06	9.09×10^{2}	4.43×10^{-6}	9.71×10^{-2}	2.35×10^{-2}	3.60×10^{-3}	3.92
Ardeotis kori	9.13×10^{3}	0.85	5.70×10^{2}	1.25×10^{-6}	6.07×10^{-2}	9.40×10^{-3}	1.40×10^{-3}	18.88
Parus major	1.08×10^{4}	8.23	4.29×10^{3}	2.16×10^{-5}	0.50	0.15	2.27×10^{-2}	0.30
Pelecanus onocrotalus	1.41×10^{4}	2.16	8.12×10^{2}	8.30×10^{-7}	7.77×10^{-2}	1.60×10^{-2}	2.40×10^{-3}	8.04
Phaethon rubricauda	1.39×10^{4}	4.46	1.64×10^{3}	6.75×10^{-6}	0.18	4.37×10^{-2}	6.70×10^{-3}	1.91
Phoeniconaias minor	1.44×10^{4}	3.93	1.35×10^{3}	8.18×10^{-5}	0.15	3.47×10^{-2}	5.30×10^{-3}	2.71
Ramphastos toco	1.18×10^{4}	2.37	1.58×10^{3}	1.44×10^{-6}	0.18	3.85×10^{-2}	5.80×10^{-3}	3.13
Podilymbus podiceps	8.84×10^{3}	3.26	1.27×10^{3}	7.46×10^{-5}	0.14	3.51×10^{-2}	5.40×10^{-3}	2.13
Diomedea exulans	2.48×10^{4}	1.48	1.68×10^{3}	4.03×10^{-7}	0.13	1.88×10^{-2}	2.80×10^{-3}	9.95
Forpus passerinus	6.03×10^{3}	4.45	2.14×10^{3}	5.24×10^{-5}	0.25	7.19×10^{-2}	1.12×10^{-2}	0.63
Pterocles alchata	8.59×10^{3}	2.70	1.38×10^{3}	1.97×10^{-5}	0.12	3.10×10^{-2}	4.80×10^{-3}	2.30
Pygoscelis adeliae	2.85×10^{4}	5.56	1.88×10^{3}	9.40×10^{-7}	0.14	3.46×10^{-2}	5.30×10^{-3}	2.72
Tyto alba	9.72×10^{3}	1.37	1.65×10^{3}	6.78×10^{-6}	0.15	3.09×10^{-2}	4.60×10^{-3}	4.30
Phalacrocorax auritus	2.18×10^{4}	4.91	2.04×10^{3}	2.60×10^{-7}	0.23	5.11×10^{-2}	7.80×10^{-3}	2.18
Euptilotis neoxenus	8.78×10^{3}	3.11	1.95×10^{3}	5.47×10^{-6}	0.22	5.61×10^{-2}	8.60×10^{-3}	1.45
Apteryx mantelli	2.52×10^{3}	1.00	1.63×10^{2}	5.05×10^{-4}	1.64×10^{-2}	4.50×10^{-3}	7.00×10^{-4}	15.48
Dromaius novaehollandiae	1.40×10^{4}	0.59	5.61×10^{2}	3.10×10^{-5}	5.69×10^{-2}	5.60×10^{-3}	8.00×10^{-4}	42.42
Rhea americana	6.61×10^{3}	1.04	2.65×10^{2}	6.01×10^{-5}	2.67×10^{-2}	5.50×10^{-3}	8.00×10^{-4}	23.99
Struthio camelus	1.93×10^{4}	1.06	5.37×10^{2}	4.11×10^{-7}	4.80×10^{-2}	6.10×10^{-3}	9.00×10^{-4}	33.88
Rhynchotus rufescens	5.53×10^{3}	0.98	7.09×10^{2}	1.38×10^{-6}	7.20×10^{-2}	1.54×10^{-2}	2.30×10^{-3}	7.92
$\bar{x}$	1.28×10^{4}	3.38	1.60×10^{3}	6.01×10^{-4}	0.16	3.94×10^{-2}	6.06×10^{-3}	6.49
SE	1.13×10^{3}	0.37	155.46	4.24×10^{-4}	1.63×10^{-2}	4.80×10^{-3}	7.51×10^{-4}	1.45
$\tilde{x}$	1.08×10^{4}	3.01	1.38×10^{3}	8.22×10^{-6}	0.14	3.19×10^{-2}	4.75×10^{-3}	3.10
Q_1	7.82×10^{3}	1.38	826.11	1.56×10^{-6}	8.13×10^{-2}	1.86×10^{-2}	8.10×10^{-3}	1.72
Q_3	1.64×10^{4}	4.58	2.02×10^{3}	7.04×10^{-5}	0.22	5.27×10^{-2}	2.85×10^{-3}	6.96
c_v	0.56	0.69	0.62	4.46	0.64	0.77	0.78	1.41

Table 3.7 – Mass-specific maturity densities estimated for each of the three main maturity thresholds in avian life cycles – birth (hatching), fledging and puberty – and respective ratios (puberty/birth and fledging/birth) coupled with the altriciality index values calculated (also puberty/birth and fledging/birth), at the reference temperature (T_{ref} = 293 K). The parameter abbreviations and their corresponding names are the following: L_b – structural length at birth (hatching); L_x – structural length at fledging; L_p – structural length at puberty; $[M_V]$ – volume-specific structural mass ($[M_V] = d_V^d/w_V$) (mol cm^{-3}); M_V^b – structural mass at birth (hatching) ($M_V^b = [M_V] \times L_b^3$) (mol); M_V^x – structural mass at fledging ($M_V^x = [M_V] \times L_x^3$) (mol); M_V^p – structural mass at puberty ($M_V^p = [M_V] \times L_p^3$) (mol); μ_H^b – dry mass-specific maturity at birth (hatching) ($\mu_H^b = E_H^b / M_V^b$) (J mol^{-1}); μ_H^x – dry mass-specific maturity at fledging ($\mu_H^x = E_H^x / M_V^x$) (J mol^{-1}); μ_H^p – dry mass-specific maturity at puberty ($\mu_H^p = E_H^p / M_V^p$) (J mol^{-1}); s^{pb}_H – puberty/birth altriciality index ($s^{pb}_H = E_H^p / E_H^b$) (-); s^{xb}_H – fledging/birth altriciality index ($s^{xb}_H = E_H^x / E_H^b$) (-); μ_H^p / μ_H^b – puberty/birth dry mass-specific maturity densities ratio (-); μ_H^x / μ_H^b – fledging/birth dry mass-specific maturity densities ratio (-).

Species	L_b (cm)	L_x (cm)	L_p (cm)	$[M_V]$ (mol cm^{-3})	M_V^b (mol)	M_V^x (mol)	M_V^p (mol)	μ_H^b (J mol^{-1})	μ_H^x (J mol^{-1})	μ_H^p (J mol^{-1})	s^{pb}_H (-)	s^{xb}_H (-)	μ_H^p / μ_H^b (-)	μ_H^x / μ_H^b (-)
Aquila chrysaetos	4.09	12.80	14.01	1.76×10^{-2}	1.20	36.87	48.28	1.31×10^{3}	6.54×10^{3}	1.92×10^{5}	5.92×10^{3}	1.54×10^{2}	1.47×10^{2}	5.00
Anas platyrhynchos	2.80	7.93	8.95	1.38×10^{-2}	0.30	6.88	9.90	8.55×10^{3}	3.56×10^{4}	1.64×10^{5}	6.30×10^{2}	94.76	19.24	4.17
Apus apus	1.37	3.23	3.29	1.80×10^{-2}	4.63×10^{-2}	0.61	0.64	1.53×10^{3}	1.20×10^{4}	1.29×10^{5}	1.17×10^{3}	1.03×10^{2}	84.13	7.85
Bucorvus leadbeateri	2.98	10.78	11.70	1.76×10^{-2}	0.47	22.04	28.16	1.19×10^{3}	5.97×10^{3}	9.91×10^{3}	5.04×10^{2}	2.38×10^{2}	8.35	5.03
Podargus strigoides	2.21	6.00	7.16	1.80×10^{-2}	0.20	3.88	6.61	1.39×10^{3}	4.56×10^{3}	3.25×10^{4}	7.92×10^{2}	65.24	23.40	3.28
Cariama cristata	3.45	8.03	12.30	1.80×10^{-2}	0.74	9.30	33.50	1.46×10^{3}	3.09×10^{3}	2.31×10^{4}	7.14×10^{2}	26.53	15.76	2.11
Larus argentatus	3.43	7.78	8.48	1.51×10^{-2}	0.61	7.09	9.17	3.67×10^{3}	1.79×10^{4}	7.51×10^{6}	3.09×10^{4}	56.86	2.04×10^{3}	4.86
Ciconia ciconia	3.51	12.27	12.51	1.59×10^{-2}	0.69	29.39	31.16	1.56×10^{3}	1.52×10^{4}	2.32×10^{6}	6.75×10^{4}	4.18×10^{2}	1.48×10^{3}	9.74
Urocolius macrourus	1.25	2.65	3.60	1.59×10^{-2}	3.10×10^{-2}	0.30	0.74	6.43×10^{3}	1.53×10^{4}	1.50×10^{5}	5.58×10^{2}	22.81	23.41	2.39
Columba livia	2.29	5.61	6.19	1.88×10^{-2}	0.23	3.32	4.47	4.55×10^{3}	1.94×10^{4}	8.83×10^{4}	3.82×10^{2}	62.28	19.38	4.25
Todiramphus cinnamominus	1.67	3.46	3.72	1.42×10^{-2}	6.68×10^{-2}	0.59	0.73	5.27×10^{3}	2.46×10^{4}	1.13×10^{5}	2.37×10^{2}	41.23	21.52	4.66
Cuculus canorus	1.28	4.08	4.53	1.51×10^{-2}	3.17×10^{-2}	1.02	1.40	1.47×10^{3}	6.24×10^{3}	3.56×10^{4}	1.07×10^{3}	1.37×10^{2}	24.26	4.26
Rhynochetos jubatus	3.55	8.69	9.02	1.80×10^{-2}	0.80	11.82	13.21	7.02×10^{3}	3.83×10^{4}	9.22×10^{4}	2.16×10^{2}	80.51	13.14	5.46
Falco naumanni	2.04	4.84	4.99	1.80×10^{-2}	0.15	2.04	2.24	2.06×10^{3}	1.39×10^{4}	1.79×10^{5}	1.28×10^{3}	90.04	86.76	6.73
Gallus gallus	2.55	3.25	8.14	1.59×10^{-2}	0.26	0.55	8.56	2.81×10^{4}	3.34×10^{4}	9.76×10^{4}	1.13×10^{2}	2.48	3.47	1.19
Gavia immer	3.74	12.54	13.85	1.67×10^{-2}	0.88	32.99	44.50	1.13×10^{3}	5.42×10^{3}	3.10×10^{4}	1.39×10^{3}	1.80×10^{2}	27.41	4.79
Gallinula chloropus	2.12	5.38	6.04	1.30×10^{-2}	0.12	2.02	2.86	1.32×10^{4}	5.49×10^{4}	3.36×10^{5}	5.85×10^{2}	67.49	25.38	4.15
Leptosomus discolor	1.16	3.06	4.72	1.42×10^{-2}	2.22×10^{-2}	0.41	1.49	5.20×10^{3}	2.20×10^{3}	4.45×10^{4}	5.76×10^{2}	7.73	8.57	0.42

Mesitornis variegatus	1.51	-	4.17	1.88×10^{-2}	6.42×10^{-2}	-	1.37	5.03×10^{3}	-	7.88×10^{4}	3.34×10^{2}	-	15.65	-
Tauraco erythrolophus	2.22	3.87	5.76	1.67×10^{-2}	0.18	0.97	3.20	4.80×10^{3}	9.66×10^{3}	5.63×10^{4}	2.06×10^{2}	10.74	11.73	2.01
Opisthocomus hoazin	2.48	4.36	8.06	1.51×10^{-2}	0.23	1.25	7.90	2.49×10^{3}	4.13×10^{3}	6.14×10^{4}	8.50×10^{2}	9.02	24.67	1.66
Ardeotis kori	3.51	6.72	15.96	1.51×10^{-2}	0.65	4.56	61.23	1.50×10^{3}	2.34×10^{3}	3.96×10^{4}	2.48×10^{3}	10.91	26.37	1.56
Parus major	1.04	2.39	2.49	1.38×10^{-2}	1.53×10^{-2}	0.19	0.21	6.43×10^{3}	3.98×10^{4}	9.67×10^{5}	2.08×10^{3}	76.44	1.50×10^{2}	6.18
Pelecanus onocrotalus	3.96	13.60	17.33	1.67×10^{-2}	1.04	42.11	87.13	1.19×10^{3}	3.85×10^{3}	3.61×10^{4}	2.54×10^{3}	1.31×10^{2}	30.25	3.23
Phaethon rubricauda	3.40	8.32	8.48	1.51×10^{-2}	0.59	8.68	9.19	1.26×10^{3}	1.05×10^{4}	5.32×10^{4}	6.55×10^{2}	1.23×10^{2}	42.12	8.35
Phoeniconaias minor	3.90	10.16	10.61	1.51×10^{-2}	0.89	15.79	18.01	1.31×10^{3}	8.31×10^{3}	1.25×10^{5}	1.92×10^{3}	1.12×10^{2}	95.36	6.36
Ramphastos toco	2.14	6.56	7.41	1.42×10^{-2}	0.14	4.02	5.79	1.57×10^{3}	6.95×10^{3}	2.37×10^{5}	6.27×10^{3}	1.28×10^{2}	1.51×10^{2}	4.43
Podilymbus podiceps	2.24	5.91	6.92	1.51×10^{-2}	0.17	3.10	4.99	4.60×10^{3}	1.61×10^{4}	1.13×10^{5}	7.26×10^{2}	64.20	24.59	3.50
Diomedea exulans	5.37	14.68	14.72	2.09×10^{-2}	3.23	66.21	66.79	1.50×10^{3}	2.50×10^{4}	2.73×10^{5}	3.77×10^{3}	3.43×10^{2}	1.83×10^{2}	16.74
Forpus passerinus	1.17	2.64	2.77	1.38×10^{-2}	2.23×10^{-2}	0.25	0.29	1.15×10^{4}	6.48×10^{4}	2.60×10^{5}	2.99×10^{2}	64.68	22.69	5.65
Pterocles alchata	2.19	4.61	6.19	1.88×10^{-2}	0.20	1.84	4.46	2.88×10^{3}	7.05×10^{3}	7.06×10^{4}	5.51×10^{2}	22.75	24.55	2.45
Pygoscelis adeliae	3.83	10.83	15.12	2.09×10^{-2}	1.17	26.57	72.31	7.20×10^{2}	1.79×10^{3}	7.25×10^{4}	6.22×10^{3}	56.31	1.01×10^{2}	2.48
Tyto alba	2.05	5.04	5.78	1.76×10^{-2}	0.15	2.25	3.39	1.66×10^{4}	6.70×10^{4}	4.78×10^{5}	6.42×10^{2}	59.78	28.78	4.04
Phalacrocorax auritus	2.79	8.41	10.66	1.42×10^{-2}	0.31	8.46	17.22	1.13×10^{3}	3.48×10^{3}	1.56×10^{5}	7.72×10^{3}	84.51	1.39×10^{2}	3.09
Euptilotis neoxenus	2.20	4.06	4.48	1.42×10^{-2}	0.15	0.95	1.28	3.88×10^{3}	1.57×10^{4}	7.16×10^{5}	1.56×10^{3}	25.42	1.85×10^{2}	4.05
Apteryx mantelli	5.71	6.40	12.10	1.59×10^{-2}	2.95	4.18	28.19	1.95×10^{5}	2.42×10^{5}	1.59×10^{6}	77.58	1.75	8.13	1.24
Dromaius novaehollandiae	4.83	5.33	23.43	1.59×10^{-2}	1.80	2.40	2.05×10^{2}	1.38×10^{4}	1.48×10^{4}	1.62×10^{5}	1.33×10^{3}	1.43	11.70	1.07
Rhea americana	5.92	16.25	22.34	1.59×10^{-2}	3.30	68.18	1.77×10^{2}	1.65×10^{4}	3.86×10^{4}	9.06×10^{4}	2.94×10^{2}	48.26	5.48	2.33
Struthio camelus	6.60	23.00	35.74	1.80×10^{-2}	5.17	2.19×10^{2}	8.22×10^{2}	5.45×10^{3}	1.54×10^{4}	1.64×10^{5}	4.78×10^{3}	1.19×10^{2}	30.08	2.82
Rhynchotus rufescens	2.79	3.11	7.45	1.59×10^{-2}	0.34	0.48	6.58	1.15×10^{4}	1.65×10^{4}	8.90×10^{4}	1.48×10^{2}	2.01	7.74	1.44
$\bar{x}$	2.93	7.40	9.78	1.63E-02	0.74	16.73	46.27	1.02×10^{4}	2.38×10^{4}	4.36×10^{5}	4.00×10^{3}	85.68	1.35×10^{2}	4.23
SE	0.22	0.72	1.04	3.08E-04	0.17	5.99	21.08	4.83×10^{3}	6.34×10^{3}	1.94×10^{5}	1.81×10^{3}	14.17	61.24	0.47
$\tilde{x}$	2.67	6.00	8.1	1.59E-02	0.28	3.88	8.23	3.77×10^{3}	1.48×10^{4}	1.13×10^{5}	7.59×10^{2}	64.68	24.63	4.05
Q_1	2.09	4.06	5.38	1.51E-02	0.15	0.97	2.55	1.47×10^{3}	5.97×10^{3}	5.89×10^{4}	4.43×10^{2}	22.81	15.71	2.33
Q_3	3.64	10.16	12.41	1.80E-02	0.84	15.79	32.33	6.72×10^{3}	2.50×10^{4}	2.14×10^{5}	2.28×10^{3}	1.19×10^{2}	91.06	5.03
c_v	0.47	0.61	0.67	0.12	1.49	2.24	2.88	3.01	1.66	2.82	2.86	1.03	2.87	0.70

3.2.2 Ecological characterization

In order to explore the existence of patterns regarding the distribution of values observed in the estimated primary and compound DEB parameters (i.e., primary and secondary patterns) within our sample of birds, we characterized these species according to thirteen different ecological factors (Table 3.8) with the following designations: Superorder, Development type, Flight, Mating system, Parental care, Nest level, Nest type, Torpor, Foraging habitat, Migratory status, Diet, Climate and Conservation status. These factors are among those previously considered in other studies dealing with basal and field metabolic rates (Martin, 1995; McNab, 2012, 2009).

For each factor different categories were designed segregating the sampled species into different groups according to their life history. Considering the total number of species involved (N = 40), the definition of these categories had to take into account the fact that sub-samples should not be too small and therefore a maximum of four different categories for each factor was assumed.

Taxonomically, the species were divided in two categories depending on their classification at the Superorder level: Palaeognathae and Neognathae.

The main physiological factor considered was the type of development, consisting of a spectrum that includes species considered to be 'altricial' – the chicks hatch with their eyes closed and little or no down and are incapable of departing from the nest, this way requiring to be fed by the progenitors (or helpers) – which are in one end of the spectrum, and other species considered to be 'precocial' – the chicks hatch with their eyes opened, covered with down, and leave the nest within two days – which are at the opposite end of the spectrum. In between, several degrees of altriciality or precociality are considered to exist. Initially the species we classified according to the criteria presented by Ehrlich et al. (1988): altricial; semi-altricial 2; semi-altricial 1; semi-precocial; precocial 4; precocial 3; precocial 2 and precocial 1. However, due to our limited sample of species using these eight levels to define the categories would result in very low subsamples for some of these. For instance, the only species to be classified as precocial 1 was the superprecocial North Island Brown Kiwi. Taking this into consideration, only four categories were finally considered for the statistical analysis: altricial; semi-altricial (includes the two levels); semi-precocial and precocial (includes the four levels of precociality mentioned). The 'semi-altricial' and 'semi-precocial' categories may be generally characterized as follows: the first category includes those birds that hatch already covered with down but are still incapable of departing from the nest and need to be fed by the progenitors; and the second category includes those birds that hatch with eyes open, covered with down, and capable of leaving the nest soon after hatching (they can walk and often swim) but still use the nest and are fed by parents.

Regarding the ability to fly, species were classified according to three categories: the first one including all the species that are unable to fly; the second one including those species that are almost flightless; and a third one including all the species that fly.

The mating system classification was originally adopted from Lislevand et al. (2007) but only two categories were established: one including all the species that are essentially monogamous (< 5% of polygamy) or monogamous with occasional polygamy (5 – 15% of polygamy); and another one including all the species that are essentially polygynous or polyandrous as well as those that mate using a lek or through promiscuous strategies.

The predominant kind of parental care performed by progenitors (until fledging) is another factor. Originally species were classified according to categories adopted from Sibly et al. (2012) but only three categories were finally used: the first one including all the species in which a single progenitor is responsible for the majority of the parental care (a single female or a single male); a second one including all the species in which the pair of progenitors is equally involved; and a third one including all the species in which occasional or predominant cooperative breeding by a multiple number of individuals takes place. The Common Cuckoo, which uses a parasitic approach to breeding, was included in the second category considering that in most of the usually parasitized species (e.g., the White Wagtail (*Motacilla alba*), the Dunnock (*Prunella modularis*) or the Reed Warbler (*Acrocephalus scirpaceus*) hatchlings are raised by the pair or progenitors.

The level at which the nest is placed was also included as a factor. Two categories were defined: one including all the species that use nests placed at high locations above the ground and another one including all the species that use nests exclusively or occasionally placed at the ground level.

The factor related to the type of nest used for reproduction followed the classification provided by Sibly et al. (2012). However, only two categories were finally considered: one that includes all the species that build open nests and another one including all the species that build closed nests as well as those that use built or naturally occurring cavities and caves.

A factor related to the ability of using torpor within the species' thermoregulatory strategy was considered, with just two natural categories: one category including the species that use torpor and another one including all the species that do not.

Regarding the foraging habitat, species that forage mostly in marine and pelagic habitats were included in the same category. Two other categories were defined for this factor: terrestrial and freshwater.

Another factor dealt with the adoption of migratory strategies. Two categories were naturally defined: one including all the species that migrate and another one including all the species that do not.

Regarding the predominant diet assumed by each species, the original classification followed that used by Sibly et al. (2012). For the analysis only two categories were defined: one including all the species that consume mostly vegetal material (i.e., vegetation and/or seeds and/or fruits) and all the species that are fundamentally omnivorous; and another one including all the species that prey or scavenge upon other animals (i.e., faunivores that consume land vertebrates, fish or invertebrates).

Concerning the prevailing climate observed in most of the breeding range of each species, we defined a factor with three categories: one including all the species from temperate and polar regions; a second one including all the species from tropical regions; and a third one including all the species from arid regions.

Finally, concerning the conservation status of the species, species were originally classified according to the statuses provided in the IUCN Red List of Threatened Species (IUCN, 2014) that refer to the world population. However, due to the fact that only two species from our sample were are classified as being "Endangered" and none of the species included are "Critically Endangered", only three categories were adopted for analysis: the first one including all the species classified as "Least Concern"; a second one including all the species classified as

"Near Threatened"; and a third one including all the species classified as being "Vulnerable" or "Endangered".

With these ecological factors and respective categories, two caveats are required. The first caveat is that the significant differences we may observe between different categories could result from correlations and are not necessarily indicative of causative factors. It is also important to consider that correlations between two or more of these factors may exist and our observations regarding possible causes need to integrate those correlations.

The occurrence of correlations between L_∞ and the ecological factors considered as well as between the factors themselves, were tested by estimating Pearson's r coefficient whenever the necessary assumptions were fulfilled, i.e., whenever the sample pairs, besides being independent, followed a normal distribution. Normality was tested through the Shapiro–Wilk test of normality. In the cases where normality was not present, correlations were tested by estimating the Spearman's rank correlation coefficient.

Table 3.8 – Selected ecological factors and characterization of each sampled species. The development type classification was adopted according to the criteria from Ehrlich et al. (1988) and include the following categories: altricial; semi-altricial; semi-precocial and precocial. The information regarding flight capacity and the ability to exhibit torpor was gathered from the literature. The species that fly are signalled with "yes", flightless species with "no" and species that are almost flightless with "a/f". The use of torpor is signalled with "yes" or "no" depending on the species thermoregulatory strategy. The mating system classification was adopted from Lislevand et al. (2007) and include the following categories: lek or promiscuity (lek/prom); monogamy (<5% polygyny) (monog); monogamy with occasional polygyny (5–15% polygyny) (mon/pol); polyandry (polyand) and polygyny (> 15% polygyny) (polygyn). Categories for all the other factors were adopted from Sibly et al. (2012). Parental care may be provided exclusively by the male or the female; by the pair; by a larger number of birds (the species regularly breeds cooperatively, with nonparents providing care) (coop); occasionally cooperatively (occas); or through brood parasitism (paras). Nest type includes the use of caves (sheltered locations, such as caves or under ledges), cavities or open cup structures, at the ground level or at higher (high) locations. The information regarding the foraging habitat was obtained from Sibly et al. (2012) when available or from specific literature. According to the habitat where they mostly forage, species are considered to be: terrestrial, freshwater, marine or pelagic. The diet refers to the type of food constituting the majority of the adult diet and the abbreviations are as follows: invertebrates (invert); omnivory (no food type is consumed the majority of the time) (omniv); vegetation (plant material other than fruit, nectar, sap, or seeds) (veget); and vertebrates (including preying or scavenging upon land vertebrates or fish) (vertfs). The migratory status was obtained from specific literature and species are simply characterized according to their ability to migrate or not. The information regarding the breeding range climate was also gathered from the literature and the categories are the following: temperate, tropical, arid and polar. The conservation status was obtained from the IUCN Red List of Threatened Species (IUCN, 2014), refer to the world population and follow the standard abbreviations for the categories included: Least Concern (LC); Near Threatened (NT); Vulnerable (VU) and Endangered (EN).

Species	Superorder	Development type	Flight	Mating system	Parental care	Nest level	Nest type	Torpor	Foraging habitat	Diet	Migratory status	Climate	Conservation status
Aquila chrysaetos	Neognathae	semi-altricial 1	yes	monog	occas	high	open	no	terrestrial	vertfs	migrant	temperate	LC
Anas platyrhynchos	Neognathae	precocial 2	yes	monog	female	ground	open	no	freshwater	omniv	migrant	temperate	LC
Apus apus	Neognathae	altricial	yes	monog	pair	high	cavity	yes	terrestrial	invert	migrant	temperate	LC
Bucorvus leadbeateri	Neognathae	altricial	a/f	monog	coop	high	cavity	no	terrestrial	invert	nonmigrant	arid	VU
Podargus strigoides	Neognathae	semi-altricial 2	yes	monog	pair	high	open	yes	terrestrial	invert	nonmigrant	arid	LC
Cariama cristata	Neognathae	semi-altricial 1	a/f	monog	pair	high	open	no	terrestrial	invert	nonmigrant	tropical	LC
Larus argentatus	Neognathae	semi-precocial	yes	monog	pair	both	open	no	marine	omniv	migrant	temperate	LC
Ciconia ciconia	Neognathae	semi-altricial 1	yes	monog	occas	high	open	no	terrestrial	vertfs	migrant	temperate	LC
Urocolius macrourus	Neognathae	altricial	yes	mon/pol	coop	high	open	yes	terrestrial	fruit	nonmigrant	arid	LC
Columba livia	Neognathae	semi-altricial 2	yes	monog	pair	high	open	no	terrestrial	seed	nonmigrant	temperate	LC
Todiramphus cinnamominus	Neognathae	altricial	yes	monog	coop	high	cavity	no	terrestrial	invert	nonmigrant	tropical	LC
Cuculus canorus	Neognathae	altricial	yes	lek/prom	paras	high	open	no	terrestrial	invert	migrant	temperate	LC
Rhynochetos jubatus	Neognathae	semi-altricial 2	no	monog	pair	ground	open	no	terrestrial	invert	nonmigrant	tropical	EN

Falco naumanni	Neognathae	semi-altricial 2	yes	mon/pol	occas	high	cave	no	terrestrial	invert	migrant	temperate	LC
Gallus gallus	Neognathae	precocial 2	a/f	polygyn	female	both	open	no	terrestrial	omniv	nonmigrant	tropical	LC
Gavia immer	Neognathae	precocial 4	yes	monog	pair	ground	open	no	freshwater	vertfs	migrant	temperate	LC
Gallinula chloropus	Neognathae	precocial 4	a/f	monog	coop	ground	open	no	freshwater	omniv	migrant	temperate	LC
Leptosomus discolor	Neognathae	semi-altricial 2	yes	polygyn	pair	high	cavity	no	terrestrial	invert	nonmigrant	tropical	LC
Mesitornis variegatus	Neognathae	semi-precocial	a/f	monog	pair	ground	open	no	terrestrial	invert	nonmigrant	tropical	VU
Tauraco erythrolophus	Neognathae	semi-altricial 2	yes	monog	pair	high	open	no	terrestrial	fruit	nonmigrant	tropical	LC
Opisthocomus hoazin	Neognathae	semi-altricial 2	yes	monog	coop	high	open	no	terrestrial	veget	nonmigrant	tropical	LC
Ardeotis kori	Neognathae	precocial 4	yes	lek/prom	female	ground	open	no	terrestrial	omniv	nonmigrant	arid	NT
Parus major	Neognathae	altricial	yes	monog	pair	high	cavity	no	terrestrial	invert	migrant	temperate	LC
Pelecanus onocrotalus	Neognathae	altricial	yes	monog	pair	ground	open	no	freshwater	vertfs	migrant	temperate	LC
Phaethon rubricauda	Neognathae	semi-altricial 2	yes	monog	pair	ground	open	no	pelagic	vertfs	migrant	tropical	LC
Phoeniconaias minor	Neognathae	semi-precocial	yes	monog	pair	ground	open	no	freshwater	invert	migrant	tropical	NT
Ramphastos toco	Neognathae	altricial	yes	monog	pair	high	cavity	no	terrestrial	fruit	nonmigrant	tropical	LC
Podilymbus podiceps	Neognathae	precocial 4	yes	monog	occas	ground	open	no	freshwater	invert	migrant	temperate	LC
Diomedea exulans	Neognathae	semi-precocial	yes	monog	pair	ground	open	no	pelagic	invert	migrant	polar	VU
Forpus passerinus	Neognathae	altricial	yes	monog	pair	high	cavity	no	terrestrial	seed	nonmigrant	tropical	LC
Pterocles alchata	Neognathae	precocial 3	yes	monog	pair	ground	open	no	terrestrial	seed	migrant	arid	LC
Pygoscelis adeliae	Neognathae	semi-altricial 2	no	monog	pair	ground	open	no	pelagic	invert	migrant	polar	NT
Tyto alba	Neognathae	semi-altricial 2	yes	monog	pair	high	cavity	no	terrestrial	vertfs	nonmigrant	temperate	LC
Phalacrocorax auritus	Neognathae	altricial	yes	monog	pair	both	open	no	freshwater	vertfs	migrant	temperate	LC
Euptilotis neoxenus	Neognathae	altricial	yes	monog	pair	high	cavity	no	terrestrial	omniv	nonmigrant	tropical	NT
Apteryx mantelli	Palaeognathae	precocial 1	no	monog	male	ground	cave	no	terrestrial	invert	nonmigrant	temperate	EN
Dromaius novaehollandiae	Palaeognathae	precocial 3	no	polyand	male	ground	open	no	terrestrial	omniv	migrant	temperate	LC
Rhea americana	Palaeognathae	precocial 2	no	polygyn	male	ground	open	no	terrestrial	veget	nonmigrant	tropical	NT
Struthio camelus	Palaeognathae	precocial 2	no	polygyn	pair	ground	open	no	terrestrial	veget	migrant	arid	LC
Rhynchotus rufescens	Palaeognathae	precocial 3	a/f	lek/prom	male	ground	open	no	terrestrial	omniv	nonmigrant	tropical	LC

3.2.3 Statistical analysis

In order to investigate whether significant differences were present regarding each DEB parameter mentioned and between different categories within each ecological factor considered, we used the Student's t-test (for factors with two categories) or one-way analysis of variance (ANOVA) (for factors with more than two categories) whenever the required assumptions were fulfilled. Normality was tested through the Shapiro–Wilk test of normality and homocedasticity was tested through the Levene's test. Whenever any of the assumptions were not fulfilled we applied the nonparametric Mann-Whitney U test or the Kruskal–Wallis one-way analysis of variance by ranks. Tukey's test and Dunn's test of multiple comparisons were used as ad-hoc tests following the ANOVA and the Kruskal-Wallis analyses of variance, respectively. Eventual correlations between parameters were tested using the tests indicated before.

The differences observed in one or more DEB parameters and their possible role in explaining existing patterns, for each ecological factor analyzed, were discussed in the framework of previous studies and general conclusions were drawn regarding further research on the description of patterns in avian life history.

A forward stepwise multiple regression was also performed, considering each DEB parameter as the dependent variable. The categorical predictor variables corresponded to the different categories defined for the set of ecological factors analysed. The baseline categories (i.e., those with coefficient $b = 0$), corresponded to the most frequent in the sample of species. Considering the Development type, for instance, the most frequent category includes the semi-altricial species. The progressive contribution of each predictor variable was used to understand which ecological factors may explain how the estimated values of each DEB parameter are distributed, beyond the effect of body size. The effect of body size was also included as a continuous predictor variable corresponding to the ultimate structural body length (L_∞) (cm). When we consider DEB parameters that are considered to be intensive (Table 3.9), this variable is expected to explain a significant portion of the scatter. Other ecological factors may be the main explaining variables when considering design DEB parameters. Any exception or deviation from these expectations has evolutionary relevance and was further discussed.

Table 3.9 – The analysed primary and compound DEB parameters and their relationship with body size (physical meaning). Primary parameters are connected to a single underlying process and compound parameters are simple functions of parameters, typically depending on several underlying processes. DEB parameters which are intrinsically independent of body size are designated as being 'intensive', while those that are expected to scale body size are classified as 'design' parameters. The expected scaling with the ultimate structural body length for design parameters is also indicated. The dry mass-specific respiration ($-J_O$ / W_d, L g^{-1} h^{-1}) is expected to decrease with the maximum dry weight to the power ¼ (Maino et al., 2014).

Parameter	Abbreviation	Type	Physical meaning	Scales with
Surface-specific maximum assimilation rate (J d^{-1} cm^{-2})	$\{\dot{p}_{Am}\}$	primary	design	L_∞
Allocation fraction to soma (-)	κ	primary	intensive	-
Energy conductance (cm d^{-1})	$\dot{v}$	primary	intensive	-
Volume-specific somatic maintenance rate (J d^{-1} cm^{-3})	$[\dot{p}_M]$	primary	intensive	-
Maturity at birth (J)	E_H^b	primary	design	L_∞^3
Maturity at fledging (J)	E_H^x	primary	design	L_∞^3
Maturity at puberty (J)	E_H^p	primary	design	L_∞^3
Maturity maintenance rate coefficient (d^{-1})	$\dot{k}_J$	primary	intensive	-
Specific cost for structure (J cm^{-3})	$[E_G]$	primary	intensive	-
Weibull ageing acceleration (d^{-2})	$\ddot{h}_a$	primary	design	L_∞
Somatic maintenance rate coefficient (d^{-1})	$\dot{k}_M$	compound	intensive	-
Maximum reserve capacity (J cm^{-3})	$[E_m]$	compound	design	L_∞
von Bertalanffy growth rate (d^{-1})	$\dot{r}_B$	compound	design	L_∞^{-1}
Dry mass-specific respiration (L g^{-1} h^{-1})	$-J_O$ / W_d	compound	design	$W_d^{m-¼}$
Fasting capacity (d)	t_s	compound	design	L_∞
Maximum wet weight per ultimate structural volume (g cm^{-3})	W_w^m / L_∞^3	compound	design	L_∞
Initial egg mass (C-mol)	M_E^0	compound	design	L_∞^4
Specific allocation to reproduction per maximum structural volume (J d^{-1} cm^{-3})	$\dot{p}_R^m$ / L_m^3	compound	intensive	-
Maturity maintenance at puberty per maximum structural volume (J d^{-1} cm^{-3})	$\dot{p}_J^p$ / L_m^3	compound	intensive	-
Dry mass-specific maturity at birth (hatching) ($\mu_H^b = E_H^b$ / M_V^b) (J mol^{-1})	μ_H^b	compound	intensive	-
Dry mass-specific maturity at fledging ($\mu_H^x = E_H^x$ / M_V^x) (J mol^{-1})	μ_H^x	compound	intensive	-
Dry mass-specific maturity at puberty ($\mu_H^p = E_H^p$ / M_V^p) (J mol^{-1})	μ_H^p	compound	intensive	-
Puberty/birth altriciality index ($s^{pb}_H = E_H^p$ / E_H^b) (-)	s^{pb}_H	compound	intensive	-
Fledging/birth altriciality index ($s^{xb}_H = E_H^x$ / E_H^b) (-)	s^{xb}_H	compound	intensive	-

3.3 Results

3.3.1 General results

Significant, yet weak or moderate, correlations were found between the ultimate structural body length (L_∞) (cm) and Superorder (Neognathae < Palaeognathae), L_∞ and Development (altricial < precocial), L_∞ and Flight (flighted < unable to fly), L_∞ and Nest level (high < low), L_∞ and Nest type (closed < open) (Table 3.10), and L_∞ and Foraging habitat (terrestrial < marine/pelagic). For these factors, due to the correlation with body length and strictly based on DEB theory we should expect the species that correspond to the 'larger' categories to exhibit higher surface-specific assimilation rates ($\{\dot{p}_{Am}\}$) (J d^{-1} cm^{-2}), cumulated energy investments up to each maturity threshold (E_H^b, E_H^x and E_H^p) (J), Weibull ageing acceleration rates ($\ddot{h}_a$) (d^{-2}), maximum reserve capacities ($[E_m]$) (J cm^{-3}), fasting capacity (t_s, d) and initial egg mass values (M_E^0) (C-mol), as well as lower von Bertalanffy growth rates ($\dot{r}_B$) (d^{-1}) and dry mass-specific respiration values ($-J_O$ / W_d, L g^{-1} h^{-1}). Any deviation from these expected patterns should have ecological meaning and represent adaptations over the course of avian life history evolution.

We found significant differences between two or more categories of bird species for every factor considered (Table 3.11). These differences concern the full range of primary and secondary DEB parameters considered for analysis except for the case of the dry mass-specific maturity at fledging (μ_H^x, J mol^{-1}). No significant differences were found for this parameter but it was still possible to observe higher values for the Palaeognathae when compared to the Neognathae ($6.54 \times 10^{-4} > 1.77 \times 10^{-4}$ J) or for precocial species when compared to altricial species ($3.41 \times 10^{-4} > 2.25 \times 10^{-4}$ J).

The distribution of values observed for many primary and compound DEB parameters was significantly explained by body size (Table 3.12). As expected, the ultimate structural body length (L_∞) was the main explaining factor for the distribution of values observed in E_H^x, E_H^p, which are expected to scale with L_∞^3, as well as in $\ddot{h}_a$, $[E_m]$ and t_s, which are expected to scale with L_∞. Also as expected, the ultimate structural length was the main explaining factor for the distribution of values observed in M_E^0, which is expected to scale with L_∞^4 ($[E_m]$ scales with L_∞ and the volume of the neonate with L_∞^3).

The von Bertalanffy growth rate ($\dot{r}_B$) is expected to scale with L_∞^{-1} and the dry mass-specific respiration ($-J_O$ / W_d) is expected to scale with $W_d^{m\ -¼}$. For both of these properties, body size was also the main explaining factor. Maturity at birth, E_H^b, is expected to scale with L_∞^3. However, differences regarding the Superorder explained 54% of the variation observed. Coupled with the effect of body size this value is raised to 67%. By including the ratites, the Palaeognathae immediately constitute a heavier group and higher E_H^b values are expected. But even the smaller North Island Brown Kiwi provides an important contribution. Despite weighing just about 2.4 kg on average, it lays an egg that corresponds to about 19% of this value (and may lay up to six eggs per year) from where a precocial hatchling will emerge.

One other DEB parameter that is expected to scale with L is the surface-specific assimilation rate ($\{\dot{p}_{Am}\}$). However, the main factor describing the distribution of values for this parameter is the Migratory status. This factor describes about 31% of the variation observed. Coupled with the effect of differences between semi-altricial and precocial species and the effect of body

size, about 64% of the distribution is explained (Table 3.12). Besides the observed effect of body size, the occurrence of migratory habits and precociality are therefore significantly associated with high assimilation rates in birds.

Table 3.10 – Spearman rank order correlation statistics between the common logarithm ($\log_{10}$) of the ultimate structural body length (L_∞, cm) and that of each ecological factor, primary and compound DEB parameters. Statistical significance is indicated as follows: * $p < 0.05$; **** $p < 0.0001$. The parameter abbreviations and their corresponding names are the following: κ – allocation fraction to soma (-); $\dot{v}$ – energy conductance (cm d^{-1}); $[\dot{p}_M]$ – volume-specific somatic maintenance rate (J d^{-1} cm^{-3}); E_H^b – maturity at birth (hatching) (J); E_H^x – maturity at fledging (J); E_H^p – maturity at puberty (J); $\dot{k}_J$ – maturity maintenance rate coefficient (d^{-1}); $[E_G]$ – specific cost for structure (J cm^{-3}); $\ddot{h}_a$ – Weibull ageing acceleration (d^{-2}); $\{\dot{p}_{Am}\}$ – maximum specific assimilation rate (J d^{-1} cm^{-2}); $\dot{k}_M$ – somatic maintenance rate coefficient (d^{-1}); $[E_m]$ – maximum reserve capacity (J cm^{-3}); $\dot{r}_B$ – von Bertalanffy growth rate (d^{-1}); $-J_O$ / W_d – dry mass-specific respiration (L g^{-1} h^{-1}); t_s – fasting capacity (d); W_w^m / L_∞^3 – maximum wet weight per ultimate structural volume (g cm^{-3}); M_E^0 – initial egg mass (C-mol); $\dot{p}_R^m$ / L_m^3 – specific allocation to reproduction per maximum structural volume (J d^{-1} cm^{-3}); $\dot{p}_J^p$ / L_m^3 – maturity maintenance at puberty per maximum structural volume (J d^{-1} cm^{-3}); s_H^{pb} – puberty/birth altriciality index (-); s_H^{xb} – fledging/birth altriciality index (-); μ_H^b – dry mass-specific maturity at birth (hatching) ($\mu_H^b = E_H^b / M_V^b$) (J mol^{-1}); μ_H^x – dry mass-specific maturity at fledging ($\mu_H^x = E_H^x / M_V^x$) (J mol^{-1}); μ_H^p – dry mass-specific maturity at puberty ($\mu_H^p = E_H^p / M_V^p$) (J mol^{-1}); μ_H^p / μ_H^b – puberty/birth dry mass-specific maturities ratio (-); μ_H^x / μ_H^b – fledging/birth dry mass-specific maturities ratio (-).

Pair of variables ($\log_{10} L_\infty$ vs …)	*N*	*R*	*t*(*N*-2)	*p* value
Superorder	40	0.41	2.77	8.73×10^{-3} *
Development type	40	0.45	3.14	3.31×10^{-3} *
Foraging habitat	40	0.32	2.05	4.69×10^{-2} *
Nest level	40	0.52	3.71	6.65×10^{-4} *
Nest type	40	0.50	3.53	1.10×10^{-3} *
Flight	40	0.42	2.86	6.93×10^{-3} *
Migratory status	40	0.25	1.60	0.12
Climate	40	7.19×10^{-2}	0.44	0.66
Mating system	40	0.25	1.59	0.12
Parental care	40	0.29	1.90	6.56×10^{-2}
Diet	40	1.97×10^{-2}	0.12	0.90
Torpor	40	0.31	2.00	5.29×10^{-2}
Conservation status	40	0.28	1.80	8.05×10^{-2}
$\log_{10} \kappa$	40	0.33	2.16	3.71×10^{-2} *
$\log_{10} \dot{v}$	40	-0.32	-2.05	4.70×10^{-2} *
$\log_{10} [\dot{p}_M]$	40	-0.47	-3.29	2.16×10^{-3} *
$\log_{10} E_H^b$	40	0.68	5.77	1.19×10^{-6} ****
$\log_{10} E_H^x$	39	0.68	5.64	1.91×10^{-6} ****
$\log_{10} E_H^p$	40	0.82	9.00	5.91×10^{-11} ****
$\log_{10} \dot{k}_J$	40	-0.33	-2.12	4.02×10^{-2} *
$\log_{10} [E_G]$	40	0.30	1.95	5.83×10^{-2}
$\log_{10} \ddot{h}_a$	40	0.48	3.33	1.92×10^{-3} *
$\log_{10} \{\dot{p}_{Am}\}$	40	0.48	3.39	1.63×10^{-3} *
$\log_{10} \dot{k}_M$	40	-0.52	-3.75	5.89×10^{-4} *
$\log_{10} [E_m]$	40	0.71	6.29	2.25×10^{-7} ****
$\log_{10} \dot{r}_B$	40	-0.58	-4.41	8.34×10^{-5} ****
$\log_{10} (-J_O / W_d)$	40	-0.58	-4.41	8.12×10^{-5} ****
$\log_{10} t_s$	40	0.63	5.06	1.1×10^{-5} ****
$\log_{10} (W_w^m / L_\infty^3)$	40	0.69	5.95	6.58×10^{-7} ****
$\log_{10} M_E^0$	40	0.96	20.69	2.79×10^{-22} ****
$\log_{10} (\dot{p}_R^m / L_m^3)$	40	-0.58	-4.39	8.67×10^{-5} *
$\log_{10} (\dot{p}_J^p / L_m^3)$	40	-0.40	-2.68	1.08×10^{-2} *
$\log_{10} s_H^{pb}$	40	0.35	2.32	2.57×10^{-2} *
$\log_{10} s_H^{xb}$	39	0.18	1.10	0.28
$\log_{10} \mu_H^b$	40	-0.27	-1.76	8.70×10^{-2}
$\log_{10} \mu_H^x$	39	-0.26	-1.64	0.11
$\log_{10} \mu_H^p$	40	-0.14	-0.89	0.38
$\log_{10} (\mu_H^p / \mu_H^b)$	40	3.25×10^{-2}	0.20	0.84
$\log_{10} (\mu_H^x / \mu_H^b)$	39	-0.18	-1.08	0.29

Table 3.11 – Significant differences found for a set of core and compound DEB parameters at the reference temperature of 293 K and each specific average adult body temperature, between the categories established for the ecological factors used in the analysis, namely: Superorder, Development type, Flight, Mating system, Parental care, Nest level, Nest type, Torpor, Foraging habitat, Migratory status, Diet, Climate and Conservation status. The categories and respective abbreviations for each factor are the following: Superorder – "N" (Neognathae) and "P" (Palaeognathae); Development type – "a" (altricial), "sa" (semi-altricial), "sp" (semi-precocial) and "p" (precocial); Flight – "u" (unable to fly), "a" (almost flightless) and "f" (able to fly); Mating system – "m" (monogamous) and "p" (polygamous); Parental care – "s" (single progenitor), "p" (pair of progenitors), "m" (multiple individuals caring for hatchlings); Nest level – "h" (high) and "l" (low); Nest type – "o" (open) and "c" (closed); Torpor – "no" (does not exhibit torpor) and "yes" (exhibits torpor); Foraging habitat – "t" (terrestrial), "f" (freshwater) and "m/p" (marine and/or pelagic); Migratory status – "m" (migratory) and "n" (non-migratory); Diet – "v/o" (vegetal material and/or omnivorous) and "c/s" (carnivorous and/or scavengers); Climate – "te" (temperate), "tr" (tropical) and "a" (arid); Conservation status – "LC" (least concern), "NT" (near threatened) and "T" (threatened). The parameter abbreviations and their corresponding names are the following: κ – allocation fraction to soma (-); $\dot{v}$ – energy conductance (cm d^{-1}); $[\dot{p}_M]$ – volume-specific somatic maintenance rate (J d^{-1} cm^{-3}); E_H^b – maturity at birth (hatching) (J); E_H^x – maturity at fledging (J); E_H^p – maturity at puberty (J); $\dot{k}_J$ – maturity maintenance rate coefficient (d^{-1}); $[E_G]$ – specific cost for structure (J cm^{-3}); $\ddot{h}_a$ – Weibull ageing acceleration (d^{-2}); $\dot{k}_M$ – somatic maintenance rate coefficient (d^{-1}); $\{\dot{p}_{Am}\}$ – maximum specific assimilation rate (J d^{-1} cm^{-2}; $[E_m]$ – maximum reserve capacity (J cm^{-3}); $\dot{r}_B$ – von Bertalanffy growth rate (d^{-1}); $-J_O$ / W_d – dry mass-specific respiration (L g^{-1} h^{-1}); t_s – fasting capacity (d); W_w^m / L_∞^3 – maximum wet weight per ultimate structural volume (g cm^{-3}); M_E^0 – initial egg mass (C-mol); $\dot{p}_R^m$ / L_m^3 – specific allocation to reproduction per maximum structural volume (J d^{-1} cm^{-3}); $\dot{p}_J^p$ / L_m^3 – maturity maintenance at puberty per maximum structural volume (J d^{-1} cm^{-3}); $s^{pb}{}_H$ – puberty/birth altriciality index (-); $s^{xb}{}_H$ – fledging/birth altriciality index (-); μ_H^b – dry mass-specific maturity at birth (hatching) ($\mu_H^b = E_H^b$ / M_V^b) (J mol^{-1}); μ_H^x – dry mass-specific maturity at fledging ($\mu_H^x = E_H^x$ / M_V^x) (J mol^{-1}); μ_H^p – dry mass-specific maturity at puberty ($\mu_H^p = E_H^p$ / M_V^p) (J mol^{-1}); μ_H^p / μ_H^b – puberty/birth dry mass-specific maturity densities ratio (-); μ_H^x / μ_H^b – fledging/birth dry mass-specific maturity densities ratio (-). The statistical values presented depend on the kind of test applied. Whenever the assumptions were fulfilled, *t* values (Student's *t*-test) and *F* values (ANOVA) are presented. Whenever the assumptions could not be fulfilled, *U* values (Mann-Whitney *U* test) and *H* values (Kruskal–Wallis one-way analysis of variance by ranks) are presented instead.

DEB parameter	Factors with two categories	Factors with three or more categories
$\{\dot{p}_{Am}\}$	Migratory status: m > n (U (38) = 65, n_1 = 20 n_2 = 20, p = 0.000275) Diet: c/s > v/o (U (38) = 108, n_1 = 17 n_2 = 23, p = 0.017300)	Foraging habitat: t < m/p (H (2) = 6.71, N = 40, p = 0.0349) Climate: te > tr; ($F_{2,37}$ = 4.89, N = 40, p = 0.013052)
κ	Superorder: N > P (U (38) = 19, n_1 = 35 n_2 = 5, p = 0.005421) Migratory status: m > n (U (38) = 114, n_1 = 20 n_2 = 20, p = 0.020735) Diet: v/o < c/s (U (38) = 108, n_1 = 17 n_2 = 23, p = 0.005722)	Foraging habitat: t < m/p (H (2) = 6.96, N = 40, p = 0.0308) Parental care: s < p (H (2) = 8.88, N = 40, p = 0.0118)
$\dot{v}$	Nest level: h > l (U (38) = 96, n_1 = 20 n_2 = 20, p = 0.005116) Superorder: N > P (U (38) = 16, n_1 = 35 n_2 = 5, p = 0.003689) Migratory status: m > n (t (38) = 2.57, n_1 = 20 n_2 = 20, p = 0.014304) Mating system: m > p (U (38) = 16, n_1 = 32 n_2 = 8, p = 0.001976) Diet: v/o < c/s (U (38) = 108, n_1 = 17 n_2 = 23, p = 0.017300) Torpor: no < yes (U (38) = 11, n_1 = 37 n_2 = 3, p = 0.023860)	Flight: a < f (H (2) = 7.62, N = 40, p = 0.0222) Development type: p < a; sa (H (3) = 13.87, N = 40, p = 0.0031) Parental care: s < p; m (H (2) = 11.57, N = 40, p = 0.0031)
$[\dot{p}_M]$	Nest level: h > l (t (38) = 3.98, n_1 = 20 n_2 = 20, p = 0.000297) Nest type: o < c (t (38) = 2.1, n_1 = 29 n_2 = 11, p = 0.042873) Superorder: N > P (U (38) = 10, n_1 = 35 n_2 = 5, p = 0.001639) Mating system: m > p (U (38) = 38, n_1 = 32 n_2 = 8, p = 0.002476) Diet: v/o < c/s (t (38) = 2.21, n_1 = 17 n_2 = 23, p = 0.032929) Torpor: no < yes (U (38) = 10, n_1 = 37 n_2 = 3, p = 0.020848)	Flight: u < f (H (2) = 9.6, N = 40, p = 0.0082) Development type: p < a; sa ($F_{3,36}$ = 6.71, N = 40, p = 0.001077) Parental care: s < p; m (H (2) = 13.41, N = 40, p = 0.0012)
E_H^b	Nest level: h < l (U (38) = 52, n_1 = 20 n_2 = 20, p = 0.000066) Nest type: o > c (U (38) = 77, n_1 = 29 n_2 = 11, p = 0.012999) Superorder: N < P (U (38) = 3, n_1 = 35 n_2 = 5, p = 0.000592) Torpor: no > yes (U (38) = 9, n_1 = 37 n_2 = 3, p = 0.018173)	Flight: u > f (H (2) = 12.5, N = 40, p = 0.0019) Development type: a < p (H (3) = 18.55, N = 40, p = 0.0003) Parental care: s > p; m (H (2) = 11.37, N = 40, p = 0.0034)
E_H^x	Nest level: h < l (U (37) = 85, n_1 = 20 n_2 = 19, p = 0.003323) Torpor: no > yes (U (37) = 15, n_1 = 36 n_2 = 3, p = 0.042446)	Flight: u > f (H (2) = 7.24, N = 39, p = 0.0268) Conservation status: LC < T (H (2) = 7.12, N = 39, p = 0.0284)
E_H^p	Nest level: h < l (U (38) = 84, n_1 = 20 n_2 = 20, p = 0.001783) Nest type: o > c (U (38) = 90, n_1 = 29 n_2 = 11, p = 0.036616) Superorder: N < P (U (38) = 25, n_1 = 35 n_2 = 5, p = 0.011228) Migratory status: m > n (U (38) = 121, n_1 = 20 n_2 = 20, p = 0.033718) Torpor: no > yes (U (38) = 15, n_1 = 37 n_2 = 3, p = 0.039978)	Flight: u > f; a (H (2) = 9.21, N = 40, p = 0.01) Development type: a < p (H (3) = 8.57, N = 40, p = 0.042423)
$\dot{k}_J$	Migratory status: m < n (U (38) = 122, n_1 = 20 n_2 = 20, p = 0.036049)	Foraging habitat: t > m/p (H (2) = 6.35, N = 40, p = 0.0419)
$[E_G]$	*No significant differences observed*	Development type: sa > a (H (3) = 8.41, N = 40, p = 0.0382)
$\ddot{h}_a$	Nest level: h < l (U (38) = 78, n_1 = 20 n_2 = 20, p = 0.001014) Superorder: N < P (U (38) = 6, n_1 = 35 n_2 = 5, p = 0.000925) Mating system: m < p (U (38) = 30, n_1 = 32 n_2 = 8, p = 0.000978)	Flight: u > f; a (H (2) = 13.13, N = 40, p = 0.0014) Development type: p > a (H (3) = 15.18, N = 40, p = 0.0017)

	Torpor: no > yes (U (37) = 13, n_1 = 37 n_2 = 3, p = 0.031031)	Parental care: s > p; m (H (2) = 10.64, N = 40, p = 0.0034)
$\dot{k}_M$	Nest level: h > l (U (38) = 70, n_1 = 20 n_2 = 20, p = 0.000460) Nest type: o < c (t (38) = 2.39, n_1 = 29 n_2 = 11, p = 0.022172) Superorder: N > P (U (38) = 10, n_1 = 35 n_2 = 5, p = 0.001639) Mating system: m > p (U (38) = 40, n_1 = 32 n_2 = 8, p = 0.003091) Torpor: no < yes (U (38) = 15, n_1 = 37 n_2 = 3, p = 0.039978)	Flight: u < f ($F_{2,37}$ = 5.71, N = 40, p = 0.006896) Development type: p < a; sa ($F_{3,36}$ = 7.52, N = 40, p = 0.000518) Parental care: s < p; m ($F_{2,37}$ = 6.24, N = 40, p = 0.004637)
$[E_m]$	Nest level: h < l (U (38) = 115, n_1 = 20 n_2 = 20, p = 0.022271) Mating system: m < p (U (38) = 45, n_1 = 32 n_2 = 8, p = 0.005279) Torpor: no > yes (U (38) = 11, n_1 = 37 n_2 = 3, p = 0.023860)	*No significant differences observed*
$\dot{r}_B$	Nest level: h > l (U (38) = 65, n_1 = 20 n_2 = 20, p = 0.000275) Superorder: N > P (U (38) = 4, n_1 = 35 n_2 = 5, p = 0.000688) Mating system: m > p; (t (38) = 2.18, n_1 = 32 n_2 = 8, p = 0.035659) Torpor: no < yes (U (38) = 13, n_1 = 37 n_2 = 3, p = 0.031031)	Flight: u < f; ($F_{2,37}$ = 11.39, N = 40, p = 0.0034) Development type: p < a; sa (H (3) = 17.34, N = 40, p = 0.0006) Parental care: s < p; m ($F_{2,37}$ = 13.26, N = 40, p = 0.0013)
$-J_O$ / W_d	Nest level: h > l (U (38) = 66 n_1 = 20 n_2 = 20, p = 0.000305) Superorder: N > P (U (38) = 3, n_1 = 35 n_2 = 5, p = 0.000592) Mating system: m > p (U (38) = 34, n_1 = 32 n_2 = 8, p = 0.002476) Torpor: no < yes (U (38) = 12, n_1 = 37 n_2 = 3, p = 0.027243)	Flight: u < f (H (2) = 11.17, N = 40, p = 0.0038) Development type: p < a; sa (H (3) = 17.16, N = 40, p = 0.0007) Parental care: s < p; m (H (2) = 13.50, N = 40, p = 0.0012)
t_s	Nest level: h < l (U (38) = 85, n_1 = 20 n_2 = 20, p = 0.001954) Superorder: N < P (U (38) = 7, n_1 = 35 n_2 = 5, p = 0.001069) Mating system: m < p (U (38) = 34, n_1 = 32 n_2 = 8, p = 0.001570) Torpor: no > yes (U (38) = 10, n_1 = 37 n_2 = 3, p = 0.020848)	Flight: u > f (H (2) = 9.02, N = 40, p = 0.011) Development type: p > a (H (3) = 13.94, N = 40, p = 0.003) Parental care: s > p; m (H (2) = 12.45, N = 40, p = 0.002)
W_w^m / L_∞^3	Nest level: h < l (U (38) = 118 n_1 = 20 n_2 = 20, p = 0.027484) Mating system: m < p (U (38) = 45, n_1 = 32 n_2 = 8, p = 0.005279) Torpor: no > yes (U (38) = 9, n_1 = 37 n_2 = 3, p = 0.018173)	*No significant differences observed*
M_E^0	Nest type: o > c (U (38) = 67, n_1 = 29 n_2 = 11, p = 0.005325) Nest level: h < l (U (38) = 72 n_1 = 20 n_2 = 20, p = 0.000687) Superorder: N < P (U (38) = 16, n_1 = 35 n_2 = 5, p = 0.003689)	Flight: u > f; a (H (2) = 11.38, N = 40, p = 0.0034) Development type: p > a (H (3) = 10.13, N = 40, p = 0.0175)
$\dot{p}_R^m$ / L_m^3	Nest type: o < c (U (38) = 84, n_1 = 29 n_2 = 11, p = 0.023101)	*No significant differences observed*
$\dot{p}_J^p$ / L_m^3	Nest type: o < c (U (38) = 85, n_1 = 29 n_2 = 11, p = 0.024996)	*No significant differences observed*
μ_H^b	Superorder: N < P (U (38) = 15, n_1 = 35 n_2 = 15, p = 0.003235) Migratory status: m > n (U (38) = 114, n_1 = 20 n_2 = 20, p = 0.02074) Mating system: m < p (U (38) = 68, n_1 = 32 n_2 = 8, p = 0.0442365) Diet: c/s < v/o (U (38) = 88, n_1 = 23 n_2 = 17, p = 0.00342)	Foraging habitat: t > m/p (H (2) = 6.63, N = 40, p = 0.0414) Parental care: s > p (H (2) = 9.96, N = 40, p = 0.0069)
μ_H^x	*No significant differences observed*	*No significant differences observed*
μ_H^p	Nest type: o < c (U (38) = 94, n_1 = 29 n_2 = 11, p = 0.04896905)	Climate: te > a (H (2) = 6.73, N = 40, p = 0.0345)
s_H^{pb}	Migratory status: m > n (U (38) = 58, n_1 = 20 n_2 = 20, p = 0.00013)	Flight: a < f (H (2) = 6.82, N = 40, p = 0.033) Foraging habitat: t < m/p (H (2) = 6.23, N = 40, p = 0.0444) Climate: te > tr (H (2) = 8.2, N = 40, p = 0.0165)
s_H^{xb}	Superorder: N > P (U (37) = 35, n_1 = 34 n_2 = 5, p = 0.037579928) Migratory status: m > n (U (37) = 74, n_1 = 20 n_2 = 19, p = 0.001173514) Mating system: m > p (U (37) = 63, n_1 = 31 n_2 = 8, p = 0.03536045) Diet: c/s > v/o (U (37) = 85, n_1 = 22 n_2 = 17, p = 0.004044523)	Parental care: s < p; m (H (2) = 8.81, N = 39, p = 0.0122)
μ_H^p / μ_H^b	Superorder: N > P (U (37) = 27, n_1 = 35 n_2 = 5, p = 0.014138) Migratory status: m > n (U (38) = 67, n_1 = 20 n_2 = 20, p = 0.000338) Mating system: m > p (U (37) = 50, n_1 = 32 n_2 = 8, p = 0.008781)	Flight: a < f (H (2) = 11.8, N = 40, p = 0.0027) Foraging habitat: t < m/p (H (2) = 7.85, N = 40, p = 0.0198) Climate: te > tr (H (2) = 6.28, N = 40, p = 0.0432) Parental care: s < p; m (H (2) = 10.67, N = 40, p = 0.0048)
μ_H^x / μ_H^b	Superorder: N > P (U (37) = 20, n_1 = 34 n_2 = 5, p = 0.006738) Migratory status: m > n (U (37) = 97, n_1 = 20 n_2 = 19, p = 0.009349) Mating system: m > p (U (37) = 29, n_1 = 31 n_2 = 8, p = 0.001014) Diet: c/s > v/o (U (37) = 96, n_1 = 22 n_2 = 17, p = 0.010373)	Development type: p > a (H (3) = 11.86, N = 40, p = 0.0079) Parental care: s < p; m (H (2) = 10.5, N = 39, p = 0.0053)

Table 3.12 – Multiple regression results considering the common logarithm ($\log_{10}$) of each DEB parameter as the dependent variable. The predictor variables correspond to different categories of the set of ecological factors analysed. The categories and respective abbreviations for each factor are the following (with the baseline categories, with coefficient $b = 0$, corresponding to the most predominant in the sample of species, signalled with an asterisk): Superorder – "N" (Neognathae*) and "P" (Palaeognathae); Development type – "a" (altricial*), "sa" (semi-altricial), "sp" (semi-precocial) and "p" (precocial); Flight – "u" (unable to fly), "a" (almost flightless) and "f" (able to fly); Mating system – "m" (monogamous*) and "p" (polygamous); Parental care – "s" (single progenitor), "p" (pair of progenitors*), "m" (multiple individuals caring for hatchlings); Nest level – "h" (high*) and "l" (low); Nest type – "o" (open*) and "c" (closed); Torpor – "no" (does not exhibit torpor*) and "yes" (exhibits torpor); Foraging habitat – "t" (terrestrial*), "f" (freshwater) and "m/p" (marine and/or pelagic); Migratory status – "m" (migratory*) and "n" (non-migratory); Diet – "v/o" (vegetal material and/or omnivorous) and "c/s" (carnivorous and/or scavengers*); Climate – "te" (temperate*), "tr" (tropical) and "a" (arid); Conservation status – "LC" (least concern*), "NT" (near threatened) and "T" (threatened). The parameter abbreviations and their corresponding names are the following: L_∞ – ultimate (adult) structural length (cm); $\{\dot{p}_{Am}\}$ – maximum specific assimilation rate (J d^{-1} cm^{-2}); κ – allocation fraction to soma (-); $\dot{v}$ – energy conductance (cm d^{-1}); $[\dot{p}_M]$ – volume-specific somatic maintenance rate (J d^{-1} cm^{-3}); E_H^b – maturity at birth (hatching) (J); E_H^x – maturity at fledging (J); E_H^p – maturity at puberty (J); $\dot{k}_J$ – maturity maintenance rate coefficient (d^{-1}); $[E_G]$ – specific cost for structure (J cm^{-3}); $\ddot{h}_a$ – Weibull ageing acceleration (d^{-2}); $\dot{k}_M$ – somatic maintenance rate coefficient (d^{-1}); $[E_m]$ – maximum reserve capacity (J cm^{-3}); $\dot{r}_B$ – von Bertalanffy growth rate (d^{-1}); $-J_O / W_d$ – dry mass-specific respiration (L g^{-1} h^{-1}); t_s – fasting capacity (d); W_w^m / L_∞^3 – maximum wet weight per ultimate structural volume (g cm^{-3}); M_E^0 – initial egg mass (C-mol); $\dot{p}_R^m / L_m^3$ – specific allocation to reproduction per maximum structural volume (J d^{-1} cm^{-3}); $\dot{p}_J^p / L_m^3$ – maturity maintenance at puberty per maximum structural volume (J d^{-1} cm^{-3}); s_H^{pb} – puberty/birth altriciality index (-); s_H^{xb} – fledging/birth altriciality index (-); μ_H^b – dry mass-specific maturity at birth (hatching) ($\mu_H^b = E_H^b / M_V^b$) (J mol^{-1}); μ_H^x – dry mass-specific maturity at fledging ($\mu_H^x = E_H^x / M_V^x$) (J mol^{-1}); μ_H^p – dry mass-specific maturity at puberty ($\mu_H^p = E_H^p / M_V^p$) (J mol^{-1}); μ_H^p / μ_H^b – puberty/birth dry mass-specific maturities ratio (-); μ_H^x / μ_H^b – fledging/birth dry mass-specific maturities ratio (-). The second κ value refers to a sample of 38 species that excludes the outlying values from the North Island Brown Kiwi (*Apteryx mantelli*) and the Red Junglefowl (*Gallus gallus*).

DEB parameter	*N*	*F*	*df*	*p*	1st Factor	r^2	b	2nd Factor	r^2	b	3rd Factor	r^2	b	4th Factor	r^2	b
$\log_{10}\{\dot{p}_{Am}\}$	40	18.97	4,35	$p < 0.0001$	Migratory: n	0.31	-0.54	Development: p	0.41	-0.59	$\log_{10} L_\infty$	0.64	0.555	Development: sp	0.68	-0.22
$\log_{10}\kappa$	40	8.07	4,35	$p < 0.0001$	Superorder: P	0.23	-0.27	Conservation: T	0.36	-0.33	Nest type: c	0.42	-0.28	Parental care: s	0.48	-0.32
$\log_{10}\kappa$	38	8.45	4,33	$p < 0.0001$	Superorder: P	0.25	-0.42	$\log_{10} L_\infty$	0.42	0.591	Parental care: s	0.47	-0.33	Flight: u	0.51	-0.28
$\log_{10}\dot{v}$	40	11.5	4,35	$p < 0.0001$	Mating: p	0.31	-0.51	Conservation: T	0.46	-0.45	Diet: v/o	0.53	-0.28	Development: a	0.57	0.211
$\log_{10}[\dot{p}_M]$	40	18.56	4,35	$p < 0.0001$	Parental care: s	0.42	-0.28	$\log_{10} L_\infty$	0.50	-0.3	Migratory: n	0.60	-0.46	Nest level: l	0.68	-0.38
$\log_{10} E_H^b$	40	29.49	4,35	$p < 0.0001$	Superorder: P	0.54	0.515	$\log_{10} L_\infty$	0.67	0.288	Development: a	0.72	-0.25	Conservation: T	0.77	0.218
$\log_{10} E_H^x$	39	16.1	4,34	$p < 0.0001$	$\log_{10} L_\infty$	0.45	0.637	Mating: p	0.57	-0.41	Conservation: T	0.62	0.208	Superorder: P	0.65	0.256
$\log_{10} E_H^p$	40	23.47	4,35	$p < 0.0001$	$\log_{10} L_\infty$	0.64	0.691	Development: sp	0.67	0.228	Flight: a	0.70	-0.2	Superorder: P	0.73	0.191
$\log_{10}\dot{k}_J$	40	5.47	4,35	$p < 0.05$	Migratory: n	0.15	0.492	Diet: v/o	0.22	-0.47	Development: p	0.31	0.475	$\log_{10} L_\infty$	0.38	-0.31

$\log_{10}[E_G]$	40	5.9	4,35	$p < 0.05$	Conservation: T	0.14	0.31	Development: a	0.25	-0.41	Parental care: s	0.33	-0.31	Foraging habitat: f	0.40	-0.28
$\log_{10}\ddot{h}_a$	40	13.51	4,35	$p < 0.0001$	$\log_{10} L_\infty$	0.37	0.475	Migratory: n	0.47	0.402	Nest level: l	0.55	0.285	Torpor: yes	0.61	-0.25
$\log_{10}\dot{k}_M$	40	20.7	4,35	$p < 0.0001$	Parental care: s	0.38	-0.2	$\log_{10} L_\infty$	0.50	-0.37	Migratory: n	0.61	-0.49	Nest level: l	0.70	-0.4
$\log_{10}[E_m]$	40	25.17	4,35	$p < 0.0001$	$\log_{10} L_\infty$	0.63	0.733	Mating: p	0.67	0.282	Development: sp	0.72	0.252	Conservation: NT	0.74	-0.16
$\log_{10}\dot{r}_B$	40	24.41	4,35	$p < 0.0001$	$\log_{10} L_\infty$	0.43	-0.51	Parental care: s	0.59	-0.2	Migratory: n	0.68	-0.42	Nest level: l	0.74	-0.32
$\log_{10}(-J_O / W_d)$	40	29.44	4,35	$p < 0.0001$	$\log_{10} L_\infty$	0.44	-0.57	Migratory: n	0.60	-0.46	Development: p	0.72	-0.45	Development: sp	0.77	-0.23
$\log_{10} t_s$	40	32.55	4,35	$p < 0.0001$	$\log_{10} L_\infty$	0.56	0.605	Migratory: n	0.67	0.344	Mating: p	0.74	0.247	Nest level: l	0.79	0.268
$\log_{10}(W_w^m / L_\infty^3)$	40	20.37	4,35	$p < 0.0001$	$\log_{10} L_\infty$	0.52	0.706	Mating: p	0.62	0.387	Development: sp	0.66	0.241	Nest type: c	0.70	0.245
$\log_{10} M_E^0$	40	130.52	4,35	$p < 0.0001$	$\log_{10} L_\infty$	0.89	0.857	Conservation: T	0.92	0.136	Foraging habitat: m/p	0.93	0.138	Superorder: P	0.94	0.101
$\log_{10}(\dot{p}_R^m / L_m^3)$	40	20.09	4,36	$p < 0.05$	$\log_{10} L_\infty$	0.28	-0.9	Superorder: P	0.58	0.675	Climate: tr	0.65	-0.35	Climate: a	0.70	-0.22
$\log_{10}(\dot{p}_J^p / L_m^3)$	40	5.01	4,35	$p < 0.05$	Nest type: c	0.10	0.098	Flight: u	0.16	0.487	$\log_{10} L_\infty$	0.32	-0.61	Parental care: s	0.36	0.227
$\log_{10} s_H^{pb}$	40	14.52	4,35	$p < 0.0001$	Migratory: n	0.33	-0.63	Development: p	0.45	-0.63	$\log_{10} L_\infty$	0.57	0.408	Diet: v/o	0.62	0.281
$\log_{10} s_H^{xb}$	39	10.69	4,34	$p < 0.0001$	Parental care: s	0.40	-0.44	Migratory: n	0.51	-0.38	Conservation: T	0.53	0.182	Superorder: P	0.56	-0.19
$\log_{10} \mu_H^b$	40	15.25	4,35	$p < 0.0001$	Parental care: s	0.32	0.451	$\log_{10} L_\infty$	0.43	-0.61	Superorder: P	0.59	0.371	Flight: u	0.64	0.297
$\log_{10} \mu_H^x$	39	7.76	4,34	$p < 0.05$	Superorder: P	0.11	0.525	$\log_{10} L_\infty$	0.30	-0.7	Conservation: T	0.42	0.336	Nest level: l	0.48	0.295
$\log_{10} \mu_H^p$	40	4.72	4,35	$p < 0.0001$	Climate: a	0.09	-0.49	Climate: tr	0.18	-0.44	Diet: v/o	0.27	0.375	Nest type: c	0.35	0.288
$\log_{10}(\mu_H^p / \mu_H^b)$	40	12.48	4,35	$p < 0.0001$	Migratory: n	0.27	-0.62	Development: p	0.51	-0.58	Diet: v/o	0.56	0.26	Development: sp	0.59	0.166
$\log_{10}(\mu_H^x / \mu_H^b)$	39	9.91	4,34	$p < 0.0001$	Mating: p	0.34	-0.36	Migratory: n	0.46	-0.44	Development: p	0.51	-0.26	Conservation: T	0.54	0.181

3.3.2 Primary patterns

3.3.2.1 Maximum specific assimilation rate ({$\dot{p}_{Am}$}, J d^{-1} cm^{-2})

The maximum specific assimilation rate ({$\dot{p}_{Am}$}, J d^{-1} cm^{-2}) is expected to increase with increasing L_∞. We observed a significant, yet moderate, correlation between {$\dot{p}_{Am}$} and L_∞ (Table 3.10). The ninth, tenth and eleventh hypotheses of this study suggested that migratory birds, faunivores and those that inhabit temperate regions should exhibit higher assimilation rates than non-migratory, plantivores and tropical bird species, respectively. Our results confirm these differences but significant differences were also observed between terrestrial and marine/pelagic species with the first exhibiting lower assimilation rates. Although not significant, differences were also visible between species in which a single progenitor takes care of the hatchling and those in which the pair of progenitors or multiple helpers assume this responsibility (Table 3.11). This last result suggests that strategies related to parental care and the evolution of cooperative breeding in bird species may be associated with higher assimilation rates and demand cues from nestlings. Nevertheless, beyond the effect of body size, the Migratory status is the ecological factor that most significantly explains a large part of the variation observed in {$\dot{p}_{Am}$} (Table 3.12). The demand for intensive muscle development before initiating a long migratory journey, in a short amount of time – a situation commonly observed in many migratory bird species – may certainly illustrate how this strategy may have driven selective pressures towards higher {$\dot{p}_{Am}$} values in many species (Figure 3.1).

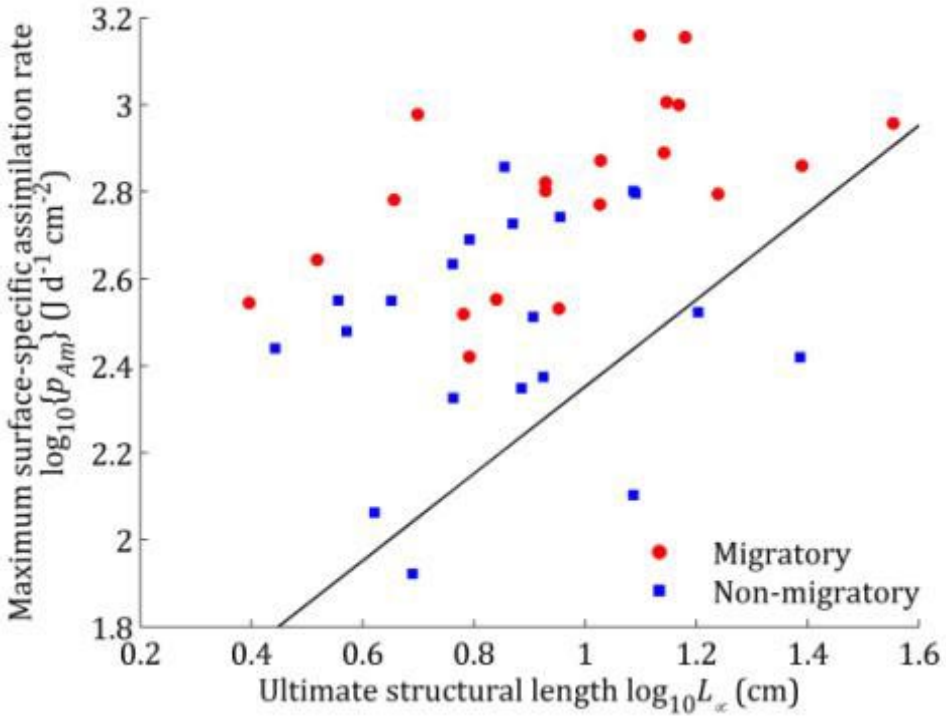

Figure 3.1 – Log-log plot of the maximum specific assimilation rate ({$\dot{p}_{Am}$}, J d^{-1} cm^{-2}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal.

3.3.2.2 Allocation fraction to soma (κ, -)

The average κ, considering the whole collection of sampled bird species, is very high (0.988), with a very low coefficient of variation (0.03) (Table 3.4) despite the cases of the North Island Brown Kiwi (*Apteryx mantelli*) and the Red Junglefowl (*Gallus gallus*) that stand out has having the lowest κ values of 0.79 and 0.96, respectively. This parameter is not expected to scale with body size but for this collection of species κ is significantly, yet weakly, correlated with L_∞ (Table 3.10). The ninth hypothesis of this study suggested higher κ values for marine or pelagic species. Our results confirm a significant difference between marine/pelagic and terrestrial bird species with the first exhibiting higher values. However, significant differences were found between categories of several other ecological factors (Table 3.11). Among these, the differences regarding the Superorder explain the most significant amount of variation in the values (about 23%) (Table 3.12). The Conservation status complements this factor and together these factors explain 36% of the variation. The five bird species classified as being threatened exhibit lower κ values. If we exclude the cases of the North Island Brown Kiwi and of the Red Junglefowl, differences regarding the Supeorder and body size together explain about 42% of the variation observed (Figure 3.2).

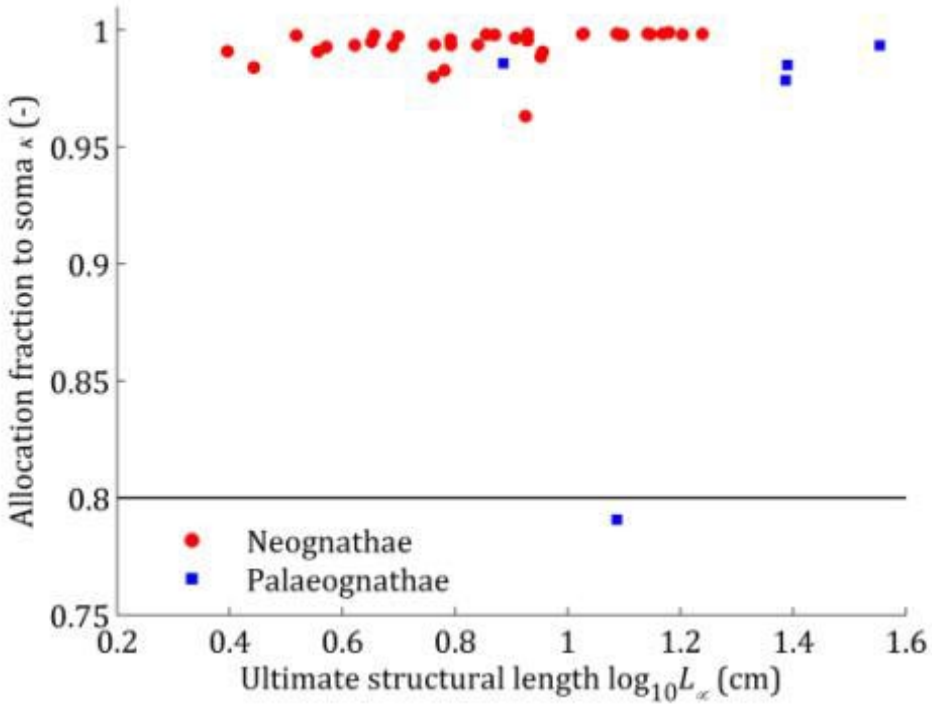

Figure 3.2 – The allocation fraction to soma (κ, -) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal.

3.3.2.3 Energy conductance ($\dot{v}$, cm d^{-1})

The energy conductance ($\dot{v}$, cm d^{-1}) is another primary DEB parameter that is expected to be independent of body size. However, a significant, yet weak and negative correlation with L_∞ was observed for our collection of bird species (Table 3.10). The eighth hypothesis of our study suggested that bird species that exhibit torpor should be able to mobilise reserve at higher rates than those that are not able to apply this strategy. The tenth and twelfth hypotheses also suggested that migratory bird species and those inhabiting temperate regions should exhibit higher rates. Our results confirm these differences. However, the difference observed between temperate and tropical species is not significant. Significant differences regarding $\dot{v}$ were also observed for several other factors (Table 3.11). It is important to consider that this is one of the most variable primary DEB parameters for birds (Teixeira et al., 2015), probably expressing considerable plasticity and responding to a variety of selective pressures. Differences regarding the Mating system, the Conservation status, the Diet and the Development type, together may account for up to 57% of the variation observed (Table 3.12). The five bird species classified as being threatened exhibited lower energy conductance values than the rest. Among the analysed factors, the Mating system seems to be the most relevant to explain the variation in $\dot{v}$ with most of the species exhibiting higher mobilisation rates adopting monogamy. Considering that high mobilisation rates may have co-evolved with high post-hatching growth rates, the level of demand in parental care may have favoured monogamy as a mating strategy. On the other hand, most of the larger bird species, with slow growth, of our sample, such as several of the Palaeognathae species, are polygamous and this sampling aspect may have influenced the result (Figure 3.3).

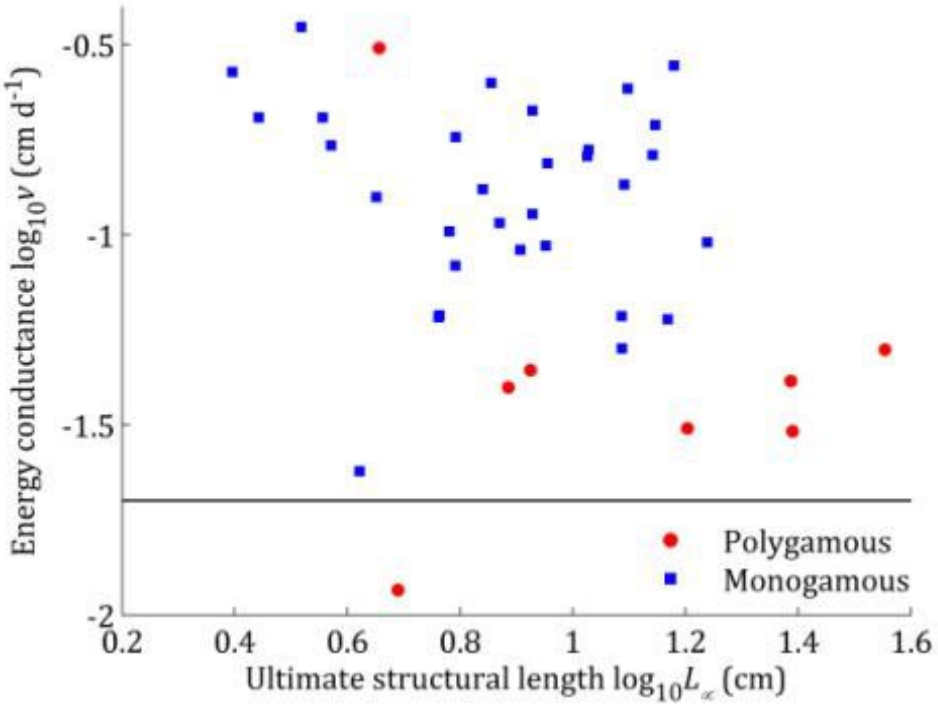

Figure 3.3 – Log-log plot of the energy conductance ($\dot{v}$, cm d^{-1}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal.

3.3.2.4 Volume-specific somatic maintenance rate ([$\dot{p}_M$], J d^{-1} cm^{-3})

The volume-specific somatic maintenance rate ([$\dot{p}_M$], J d^{-1} cm^{-3}) is also not expected to scale with body size. However, for this collection of species [$\dot{p}_M$] is significantly, yet moderately and negatively correlated with L_∞ (Table 3.10). The third and sixth hypotheses of our study suggested that flighted bird species and those that build nests in higher locations, should exhibit higher somatic maintenance costs than those that are not able to fly and use nests places in locations near the ground. The eleventh and twelfth hypotheses also suggested that birds with a plantivore diet and those that inhabit tropical regions should exhibit lower values of [$\dot{p}_M$] than those with a faunivores diet and those that inhabit temperate regions, respectively. Our results confirm these differences, which are significant except for the case of the climate for which the difference is not significant but still observable. Other significant differences regarding [$\dot{p}_M$] were observed between the categories defined by other factors (Table 3.11). This DEB parameter exhibits a moderate amount of variability in birds (Teixeira et al., 2015), and may respond to a variety of selective pressures. The difference between species with parental care provided by both progenitors and those with parental care provided by just one of the progenitors is enough to explain about 42% of the variation in [$\dot{p}_M$]. Adding the effect of body size, Migratory status and Nest level, raises this value to about 68%. Parental care seems to be the most relevant to explain the variation in [$\dot{p}_M$]. These results suggest that the emergence of increased parental care in life history strategies that include both progenitors providing food to the hatchling may have occurred in species with hatchlings exhibiting higher somatic maintenance costs, as they grow in the nest (Figure 3.4).

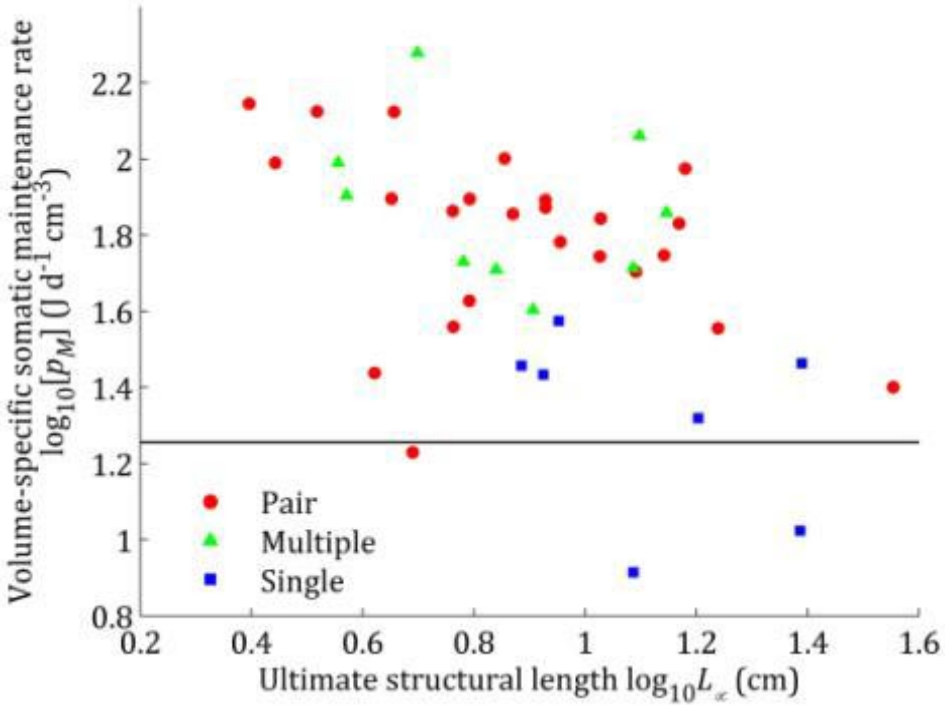

Figure 3.4 – Log-log plot of the volume-specific somatic maintenance rate ([$\dot{p}_M$], J d^{-1} cm^{-3}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal.

3.3.2.5 Maturity at birth (hatching) (E_H^b, J)

The amount of energy that has been invested in maturation up to the moment of birth (E_H^b, J) is expected to scale with L_∞^3. Our results confirm that this parameter is indeed significantly, yet moderately, correlated with L_∞ in birds (Table 3.10). The seventh hypothesis of our study suggested that differences regarding the incubation period could occur between species that use different types of nest. The nesting strategy could somehow reflect physiological or metabolic differences. We did observe a significant difference regarding the energy investment in maturation, up to birth, between species that use an open nest and those that use or build closed nests. Significant differences regarding the maturity at birth (E_H^b) (J) were also observed for other factors (Table 3.11). Just as it was observed with κ, the Superorder is the main factor explaining the variation of values we observe for E_H^b in our collection of bird species (about 54%). With L_∞, 67% of the variation is explained. Further differences related to the kind of parental care (single *vs* pair of progenitors) and the Conservation status of the species raise the value up to 75% (Table 3.12). Nevertheless, the differences we observe between the Neognathae and the Palaeognathae seem to be the most relevant to explain the diversity of values of E_H^b (Figure 3.5).

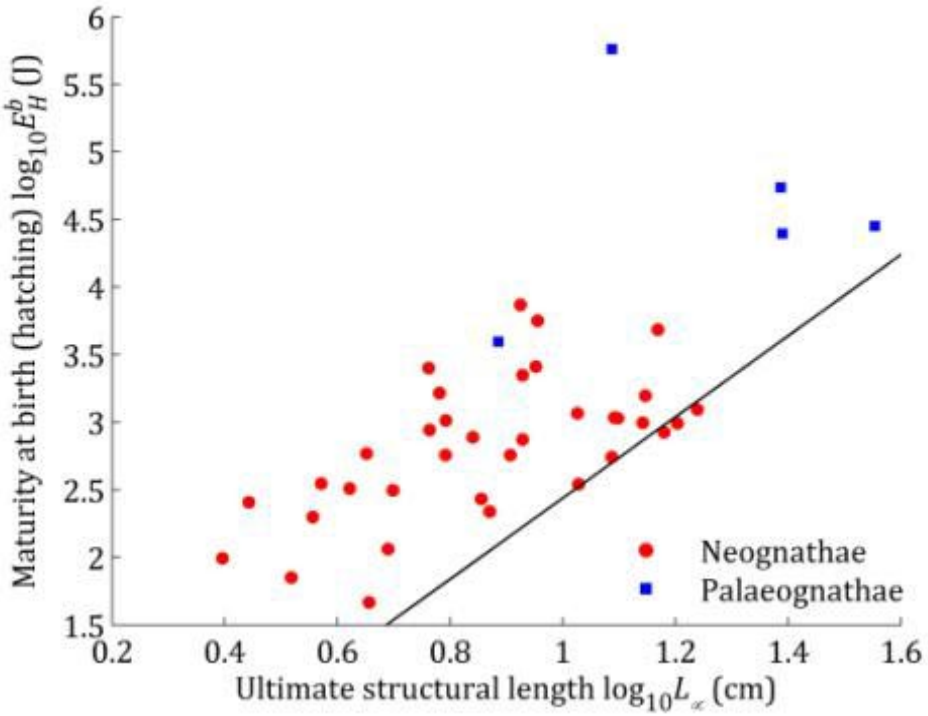

Figure 3.5 – Log-log plot of the maturity at birth (E_H^b, J) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal.

3.3.2.6 Maturity at fledging (E_H^x, J)

Just as with E_H^b, the amount of energy that has been invested in maturation up to the moment of fledging (E_H^x, J) is expected to scale with L_∞^3. Our results confirm that this parameter is indeed significantly, yet moderately, correlated with L_∞ (Table 3.10). The seventh hypothesis of our study also suggested that the use of different kinds of nesting strategies could reflect metabolic differences regarding the fledging period. No significant differences regarding the Nest type were observed but bird species that nest in lower locations exhibit significantly higher values, a result probably reflecting the effect of larger, heavier bird species which build their nests close to or on the ground. Significant differences for E_H^x were found between different categories of other factors (Table 3.11). The most relevant factor to explain the diversity of values in E_H^x was body size, which by itself explains about 45% of the variation. Beyond the effect of body size, and among the ecological factors considered, the Mating system is the most relevant one, raising the value up to about 57% (Table 3.12). Smaller species investing less energy in maturation up to the moment of fledging seem to adopt, to a certain extent, monogamy as the predominant mating system (Figure 3.6).

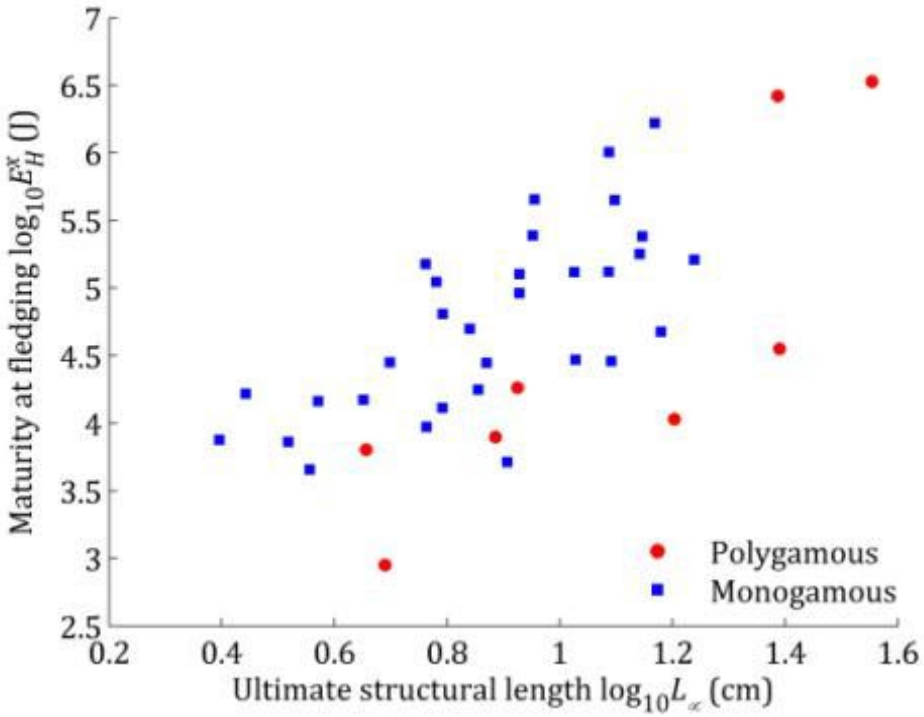

Figure 3.6 – Log-log plot of the maturity at fledging (E_H^x, J) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K.

3.3.2.7 Maturity at puberty (E_H^p, J)

Just as with E_H^b and E_H^x, the amount of energy that has been invested in maturation up to puberty (E_H^p, J) is expected to scale with L_∞^3. Our results confirm that this parameter is indeed significantly, yet moderately, correlated with L_∞ (Table 3.10). Our third and sixth hypotheses suggest that flighted species and those that build nests in higher locations should reach sexual maturity sooner than those that are unable to fly or nest in lower locations. Our results confirm both hypotheses but significant differences in E_H^p were also observed among categories of other factors (Table 3.11). Body size is enough to explain about 64% of the variation observed. Beyond this effect, differences regarding the Development type are the most relevant, despite the low amount of variation each new factor added explains (Table 3.12) (Figure 3.7).

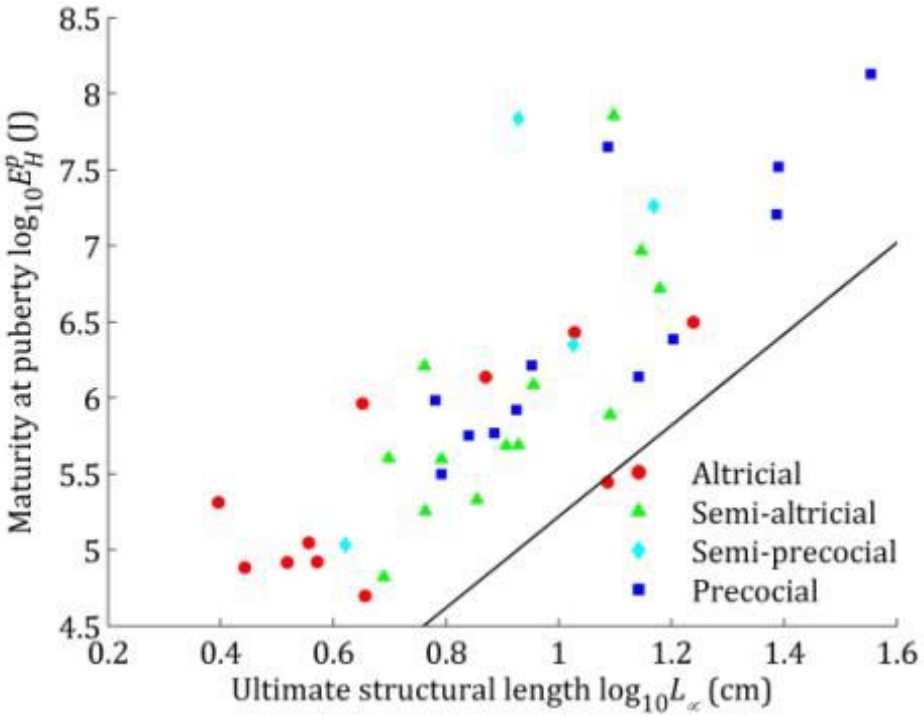

Figure 3.7 – Log-log plot of the maturity at puberty (E_H^p, J) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal.

3.3.2.8 Maturity maintenance rate coefficient ($\dot{k}_J$, d^{-1})

The maturity maintenance rate coefficient ($\dot{k}_J$, d^{-1}) is not expected to scale with body size. However, there is a significant, yet weak and negative correlation between $\dot{k}_J$ and L_∞ (Table 3.10). Our eighth hypothesis suggested that maintenance rates in bird species that exhibit torpor could be higher than in those that do not have this capacity. We did not find a significant difference in the values of $\dot{k}_J$ between these two groups of birds. However, we observed that marine or pelagic species and migratory species exhibit significantly lower values of $\dot{k}_J$ than terrestrial and non-migratory species (Table 3.11). The Migratory status explains about 15% of the variation observed. Adding further variables adds little more explaining power (Table 3.12). If there are indeed factors that may be driving the evolution regarding this parameter, they are not present on this study and acting indirectly or it may just happen that the variation of maturity maintenance rates in birds is the result of many different factors working together (Figure 3.8).

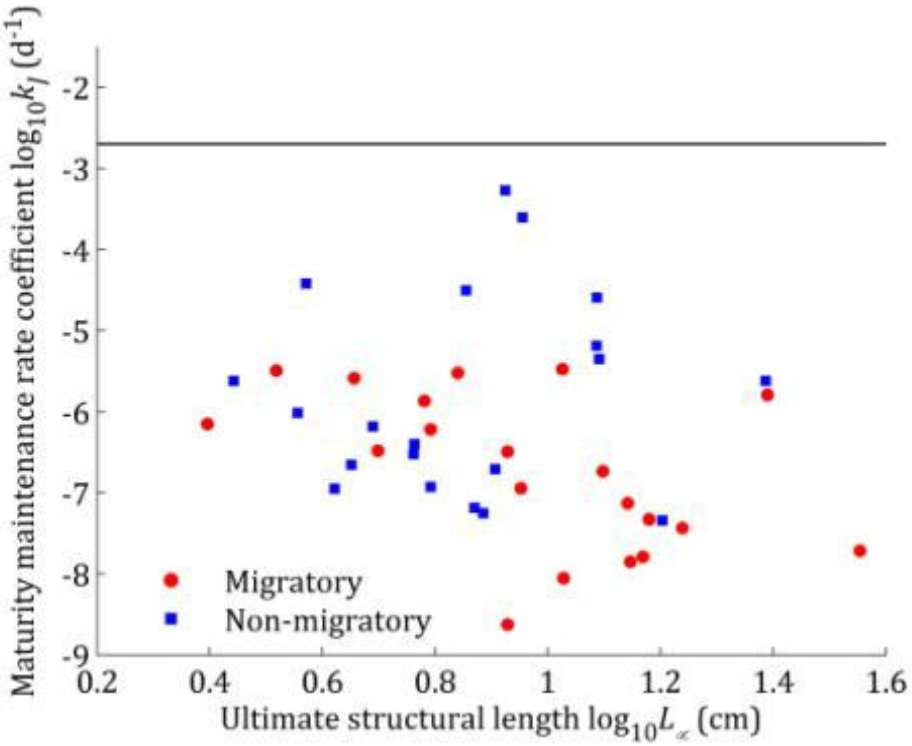

Figure 3.8 – Log-log plot of the maturity maintenance rate coefficient ($\dot{k}_J$, d^{-1}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal.

3.3.2.9 Specific cost for structure ($[E_G]$, J cm^{-3})

The specific cost for structure ($[E_G]$, J cm^{-3}) is not expected to scale with body size, and as expected we did not find any significant correlation with L_∞ (Table 3.10). The effect of a common κ_G of about 0.8 among the species, as it was used as a pseudo-data during the parameterization process in the absence of real efficiency values, constraints the variation in $[E_G]$ which will only depend on the wet weight / dry weight ratio (Teixeira et al., 2015). The only significant difference observed regarding this parameter was between semi-altricial and altricial species, due to differences in the referred ratio (Table 3.11). Almost significant was also the difference between the five threatened species of our sample and the rest, with the first exhibiting higher values. The Conservation status was the main variable, explaining about 14% of the distribution, followed by the Development type and together these variables described about 25% of the variation (Table 3.12) (Figure 3.9).

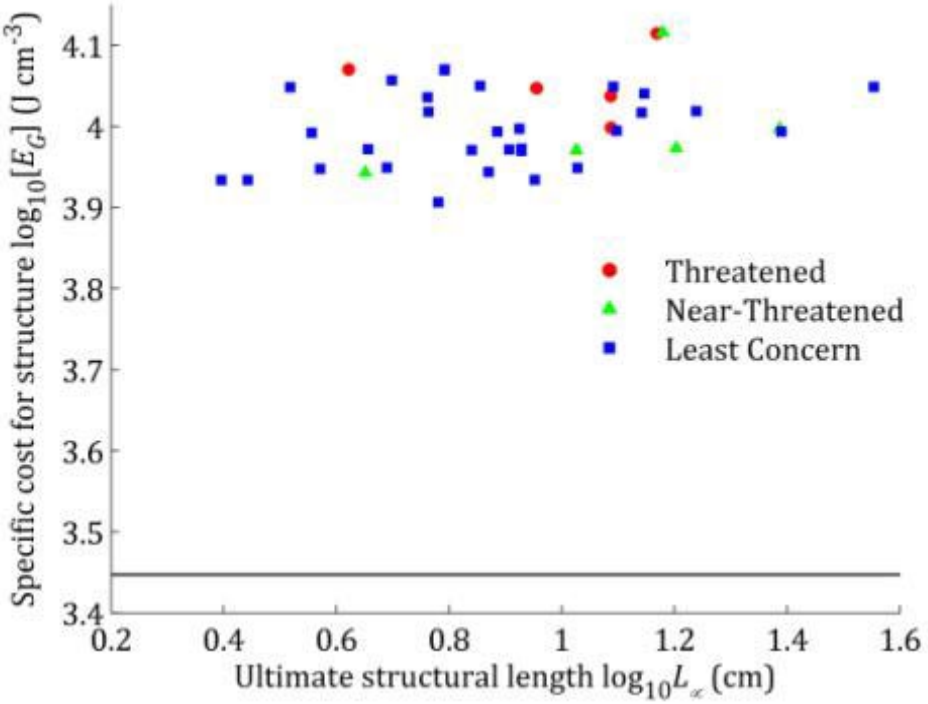

Figure 3.9 – Log-log plot of the specific cost for structure ($[E_G]$, J cm^{-3}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal, assuming a specific density of d_V = 0.1 g cm^{-3}.

3.3.2.10 Weibull ageing acceleration ($\ddot{h}_a$, d^{-2})

The Weibull ageing acceleration ($\ddot{h}_a$, d^{-2}) is another DEB parameter that is expected to increase with body size. We did observe a significant, yet moderate, correlation between this parameter and L_∞ (Table 3.10). Significant differences were found between categories of different factors (Table 3.11) but beyond the effect of body size, which explains about 37% of the variation observed in the pattern, the Migratory status was the most relevant factor and 47% of the variation is explained when we add this variable (Table 3.12). The non-migratory species of our sample exhibit higher ageing acceleration rates than migratory species. A surprising result considering that the highest physiological demands associated with migratory behaviour would suggest shorter life spans. On the other hand, the average life span duration values registered for birds in captivity, which differ from the usual observed life span in the wild, are not always available for migrating birds and therefore there is still a considerable amount of uncertainty regarding the life span of many species and a larger collection of species may offer different results (Figure 3.10).

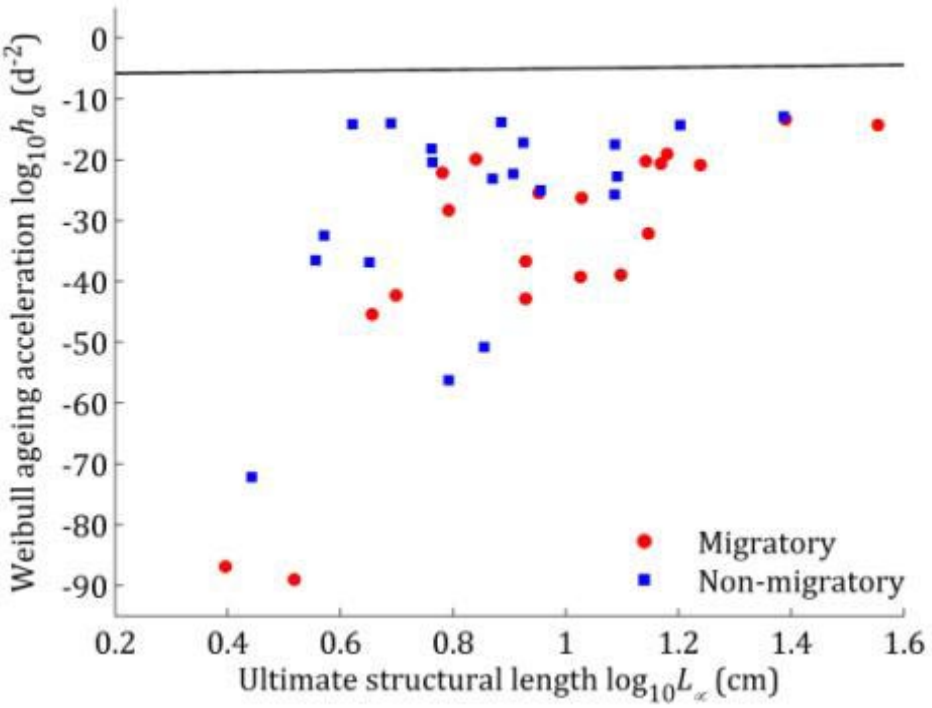

Figure 3.10 – Log-log plot of the Weibull ageing acceleration ($\ddot{h}_a$, d^{-2}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal.

3.3.3 Secondary patterns

3.3.3.1 Somatic maintenance rate coefficient ($\dot{k}_M$, d^{-1})

The somatic maintenance rate coefficient ($\dot{k}_M$, d^{-1}) is not expected to scale with body size. However, the negative correlation observed between [$\dot{p}_M$] and L_∞ also results in a similar moderate and negative correlation between $\dot{k}_M$ and L_∞ (Table 3.10). Several of the hypotheses considered in this study refer to differences in somatic maintenance rates, namely our third hypothesis, suggesting higher rates in flighted bird species, the sixth hypothesis suggesting higher rates in bird species nesting at higher locations, the eighth hypothesis suggesting higher rates in birds that exhibit torpor, the tenth hypothesis suggesting higher rates in migratory birds, the eleventh hypothesis suggesting higher rates in faunivores and the twelfth hypothesis suggesting higher rates in bird species inhabiting temperate regions. Significant differences were found between categories related with all of the factors involved in these hypotheses, except for the last three of them (Migratory status, Diet and Climate). Besides these, significant differences were found for other factors (Table 3.11). Given the relationship between [$\dot{p}_M$] and $\dot{k}_M$, it is not surprising that Parental care is the most relevant factor explaining the observed variation in $\dot{k}_M$. Species with higher somatic maintenance rates display strategies that involve more than one progenitor taking care and feeding the nestling. Adding the effect of L_∞ allows for 54% of the variation in this parameter to be described (Table 3.12) (Figure 3.11).

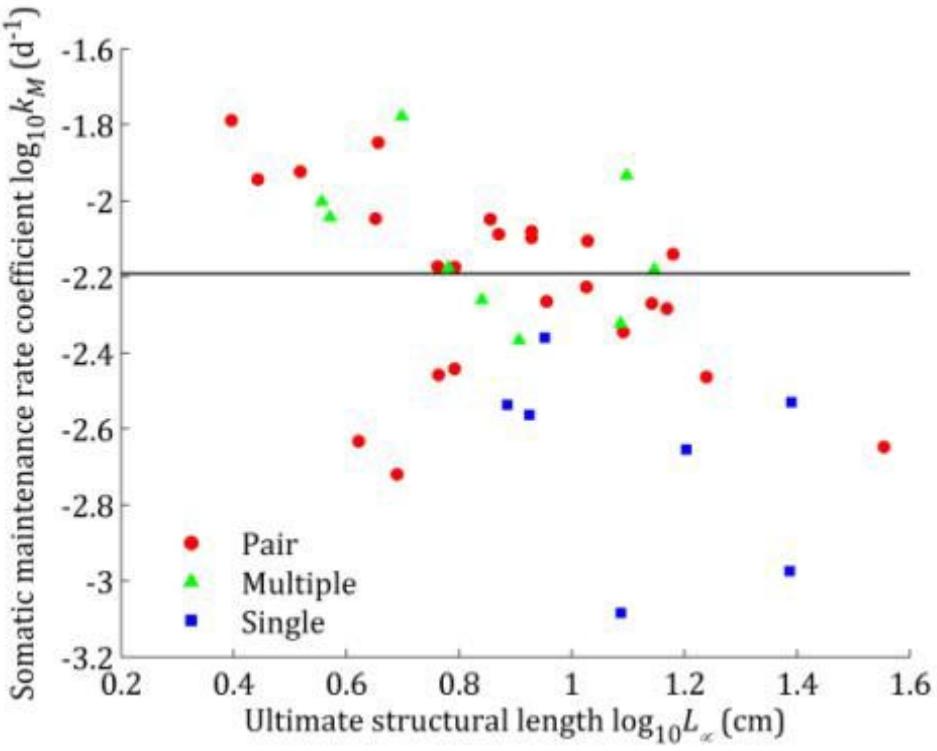

Figure 3.11 – Log-log plot of the somatic maintenance rate coefficient ($\dot{k}_M$, d^{-1}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal.

3.3.3.2 Maximum reserve capacity ([E_m], J cm^{-3})

The maximum reserve capacity ([E_m], J cm^{-3}) is expected to increase with increasing L_∞, considering the expected increase in $\{\dot{p}_{Am}\}$ and considering that $\dot{v}$ is expected to be independent from body size. In the present case, $\dot{v}$ actually decreases with L_∞ and therefore our results confirm the expected trend and a significant, strong and positive correlation between [E_m] and L_∞ was observed (Table 3.10). We also observed significant differences regarding this parameter according to several ecological factors (Table 3.11). Nevertheless, L_∞ is the most relevant factor explaining the pattern observed for this parameter. The ultimate structural body length accounts for about 63% of the variation, just by itself (Table 3.12). Beyond this effect, the second most relevant factor refers to the Mating system, with polygamous species exhibiting higher values of [E_m] (Figure 3.12).

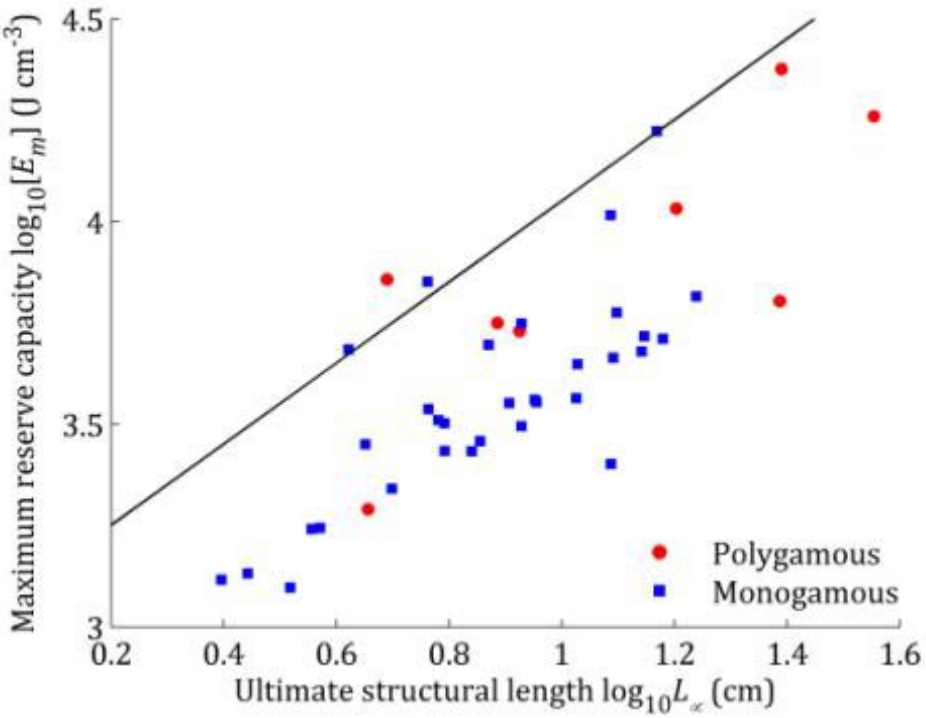

Figure 3.12 – Log-log plot of the maximum reserve capacity ([E_m], J cm^{-3}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal.

3.3.3.3 von Bertalanffy growth rate ($\dot{r}_B$, d^{-1})

The von Bertalanffy growth rate ($\dot{r}_B$, d^{-1}) is expected to decrease with increasing body size due to increasing reserve capacity, scaling with L_∞^{-1}. Our results confirm this expectation with $\dot{r}_B$ correlating moderately and negatively with L_∞ (Table 3.10). The fact that $[\dot{p}_M]$ and $\dot{k}_M$ are decreasing with L_∞ also contributes to this declining trend in growth rates. Several of our hypotheses refer to expectations regarding growth rates and we did find significant differences between categories of several factors (Table 3.11). The variable that significantly explains most of the distribution of values of this parameter is L_∞. Structural length alone describes about 43% of the variation. The degree of Parental care exhibited by the species further explains another significant part of the distribution. Coupled with body size, about 59% of the variation is accounted for. The Migratory status and the Nest level raise this value up to about 74% (Table 3.12). Species with hatchlings growing at higher rates seem to demand a higher level of parental care provided by both progenitors instead of just one or in some cases by a multiple number of juveniles and adults (cooperative breeding). Several hypotheses of this study suggested differences regarding the growth rate to occur between different categories described in several of the factors considered. Our results confirm most of these hypotheses (which included differences regarding Parental care to be expected) but no significant differences were observed regarding the use of different types of nest or the Conservation status (as the seventh and thirteenth hypotheses suggested) (Figure 3.13).

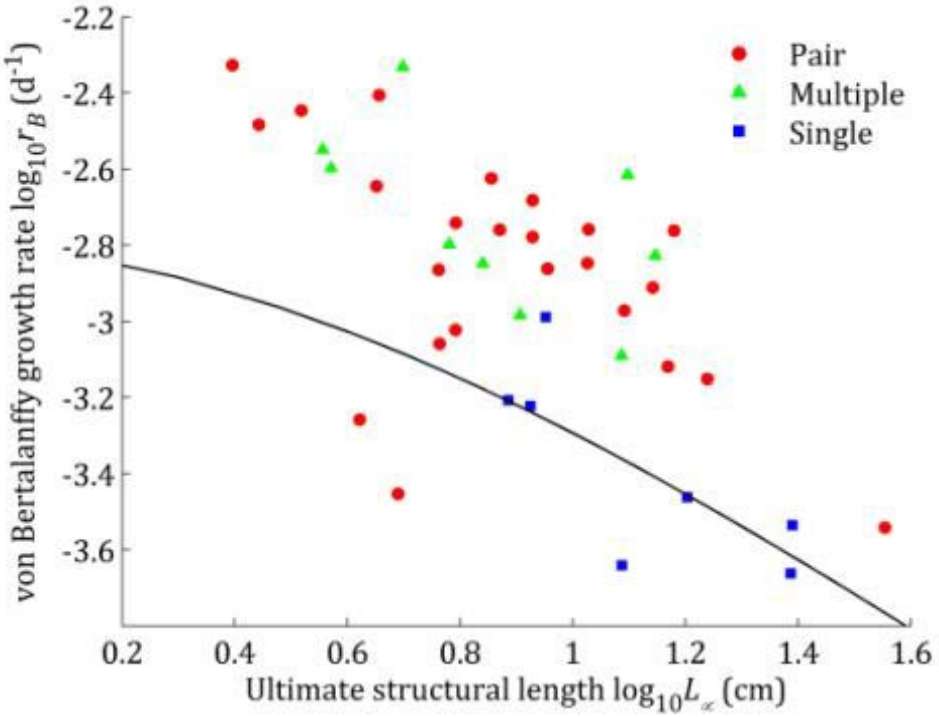

Figure 3.13 – Log-log plot of the von Bertalanffy growth rate ($\dot{r}_B$, d^{-1}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal.

3.3.3.4 Dry mass-specific respiration (-J_O / W_d, L g^{-1} h^{-1})

As it was detailed in (Teixeira et al., 2015), estimating respiration values through DEB theory requires no particular assumption and the fluxes are estimated based on the conservation of chemical elements (C, H, O and N). Every energy flux (assimilation, somatic and maturity maintenance and reproduction overheads) has an effect on these values. Previously we established that [E_m] is expected to increase with increasing L_∞ and that in the case of our sample of birds this expectation is confirmed. Due to this pattern, we may expect mass-specific respiration to decline as body size increases. Recently, Kooijman and Lika (2014a) observed that in fish the dry mass-specific respiration approximately decreases with the maximum dry weight to the power ¼. Such decrease had already been suggested (Maino et al., 2014) (Table 3.9). According to our results, the dry mass-specific respiration (-J_O / W_d, L g^{-1} h^{-1}) follows the expected pattern, decreasing with increasing L_∞. In fact there is a significant, moderate and positive correlation between this parameter and L_∞. Most of the values exhibited by the sampled bird species were below the expectations computed for the generalized animal.

Significant differences regarding this parameter were observed between categories of several factors (Table 3.11). Body size is the main variable explaining the distribution of values (Table 3.12). About 44% of the distribution is explained in this manner and the second most relevant variable is the Migratory status. Migratory birds exhibit higher mass-specific respiration values than non-migratory species. Adding the Development type allows us to describe about 77% of the scatter (Figure 3.14).

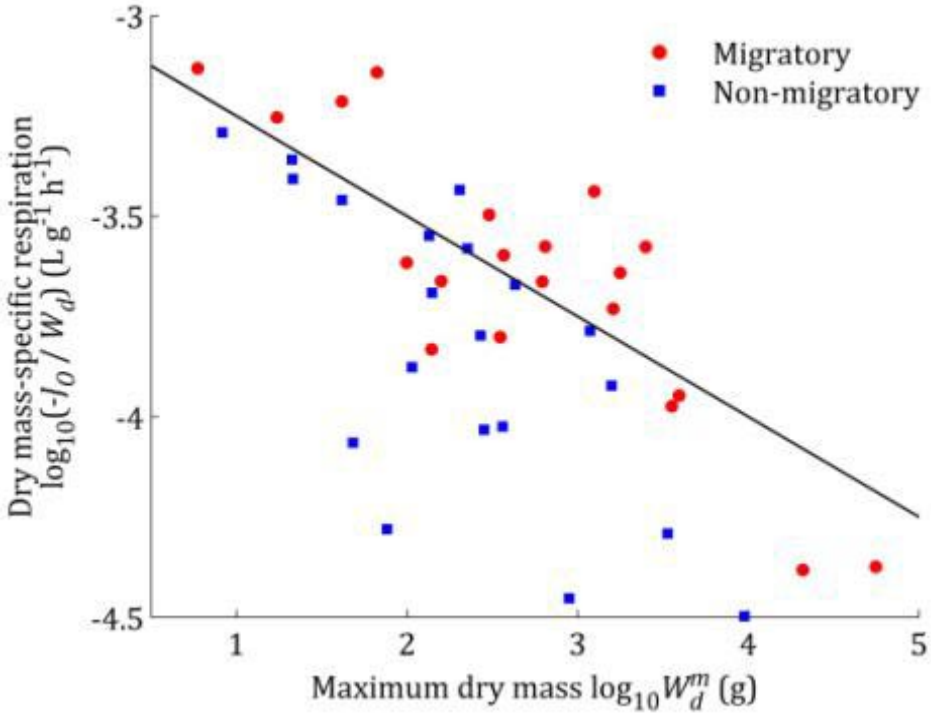

Figure 3.14 – Log-log plot of the dry mass-specific respiration (-J_O / W_d, L g^{-1} h^{-1}) as a function of the maximum dry mass (W_d^m, g) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal.

3.3.3.5 Fasting capacity (t_s, d)

The fasting capacity (t_s, d) is expected to increase with increasing body size due to increasing maximum reserve capacities. Our results confirm this pattern for birds and a significant, moderate and positive correlation between t_s and L_∞ is observable (Table 3.10). For larger birds, which are mostly flightless or almost flightless, the steeper decrease in somatic maintenance costs coupled with higher reserve capacities due to their size, provides higher fasting capacities and lower starvation risks (Teixeira et al., 2015). Significant differences regarding this parameter are also observed between categories of several factors (Table 3.11). However, beyond the effect of body size, which by itself describes about 56% of the variation observed, the Migratory status is the most relevant factor to explain the distribution of values. Adding this factor, along with the Mating system and Nest level allows for about 79% of the variation in t_s to be described (Table 3.12). Our results so far allow us to understand that migratory bird species exhibit higher assimilation and maintenance rates but lower fasting capacities than non-migratory species (Figure 3.15).

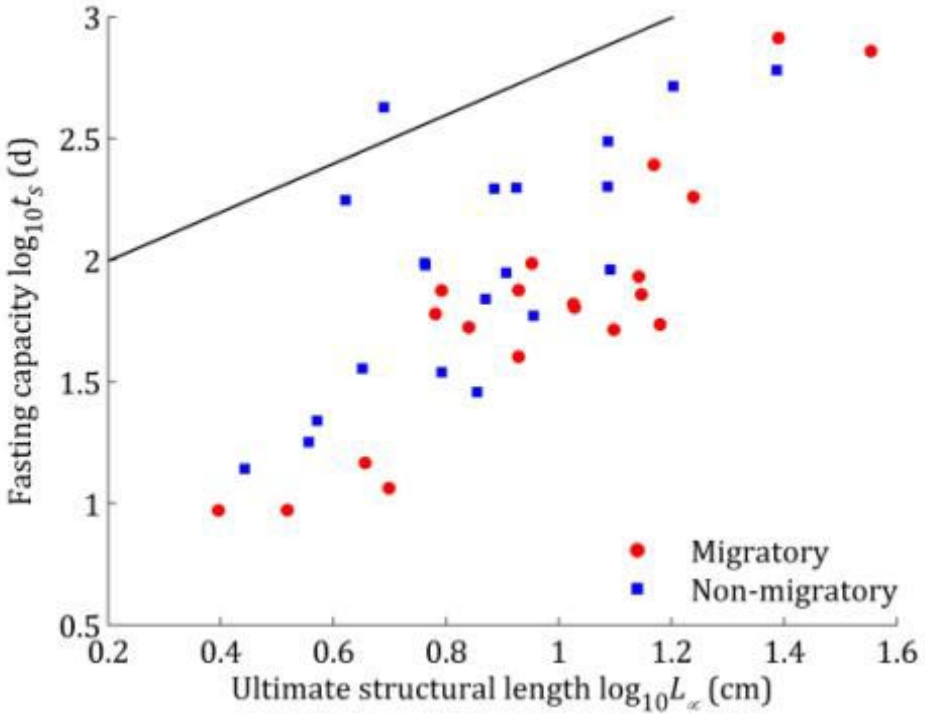

Figure 3.15 – Log-log plot of the fasting capacity (t_s, d) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal.

3.3.3.6 Maximum wet weight per ultimate structural volume (W_w^m / L_∞^3, g cm^{-3})

The maximum wet weight per ultimate structural volume (W_w^m / L_∞^3, g cm^{-3}) is expected to scale with L_∞ due to the contribution of the reserve capacity to weight ([E_m] scales with L_∞). The values computed for our sampled bird species are significantly, yet moderately, correlated with L_∞ (Table 3.10). One of the significant differences observed for this parameter concerned the Mating system, with monogamous species exhibiting higher values than polygamous species (Table 3.11). Other differences occur between species that nest in high locations and those that nest in low locations and between species that exhibit torpor and those that do not. These differences may be somewhat correlated and illustrate a context of smaller, relatively lighter, flighted bird species, that explore habitats in high locations such as canopies. Beyond the effect of body size, which explains 52% of the variation observed, the Mating system is the factor that further explains a greater share of the variation, raising this value up to about 66% (Table 3.12) (Figure 3.16).

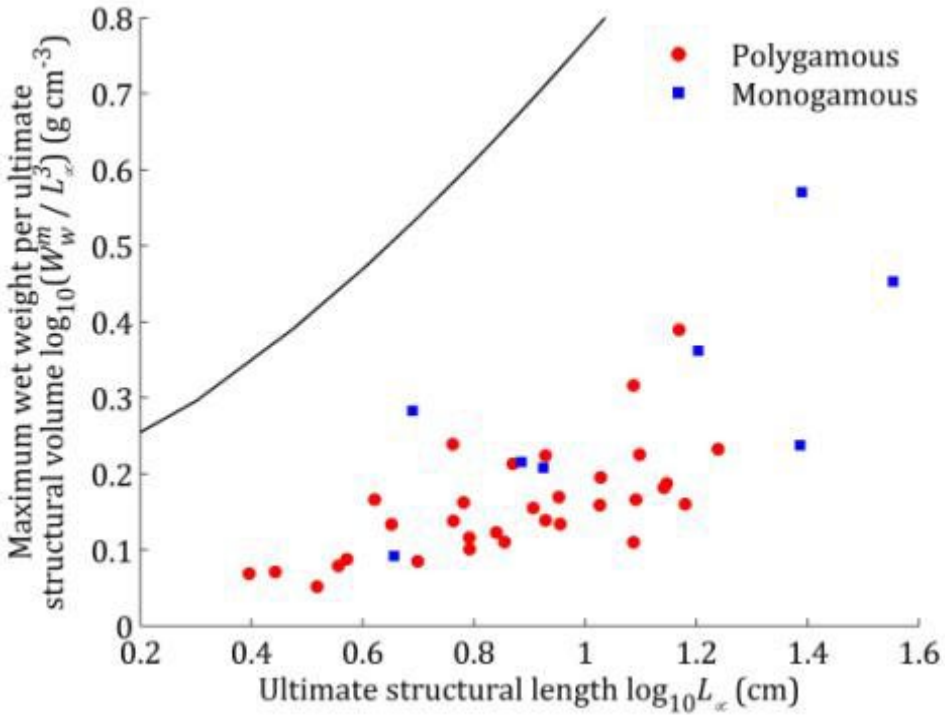

Figure 3.16 – Log-log plot of the maximum wet weight per ultimate structural volume (W_w^m / L_∞^3, g cm^{-3}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal.

3.3.3.7 Initial egg mass (M_E^0, C-mol)

The initial egg mass (M_E^0, C-mol) is expected to increase with L_∞^4 due to the fact that $[E_m]$ increases with L_∞ and the structural volume of the hatchling increases with L_∞^3. Our results confirm this pattern for birds with M_E^0 significantly and strongly correlated with L_∞ (Table 3.10) (Figure 3.17). Our second hypothesis suggested that altricial species should lay smaller eggs than precocial species. The difference is not significant but observable. Other significant differences were found for several factors (Table 3.11), but the variation is almost completely (89%) described by L_∞ (Table 3.12). However, it is interesting to note that the species of our sample that are currently classified as being Threatened lay relatively larger eggs for their body size. The Wandering Albatross (*Diomedea exulans*), for instance, shares a very similar value of L_∞ with the Golden Eagle (*Aquila chrysaetos*) (14.75 cm ≈ 14.00 cm) but has an estimated initial egg mass that is 4.54 times larger than that which is estimated for the eagle (10.39 > 2.29 C-mol). In relative terms, i.e., if we calculate M_E^0 / L_∞^3, the Wandering Albatross exhibits the highest value (3.24 C-mol cm^{-3}), which is probably a strategy that evolved to minimize the effects of returning to a fixed nesting spot (which constrains their foraging options) (Teixeira et al., 2014).

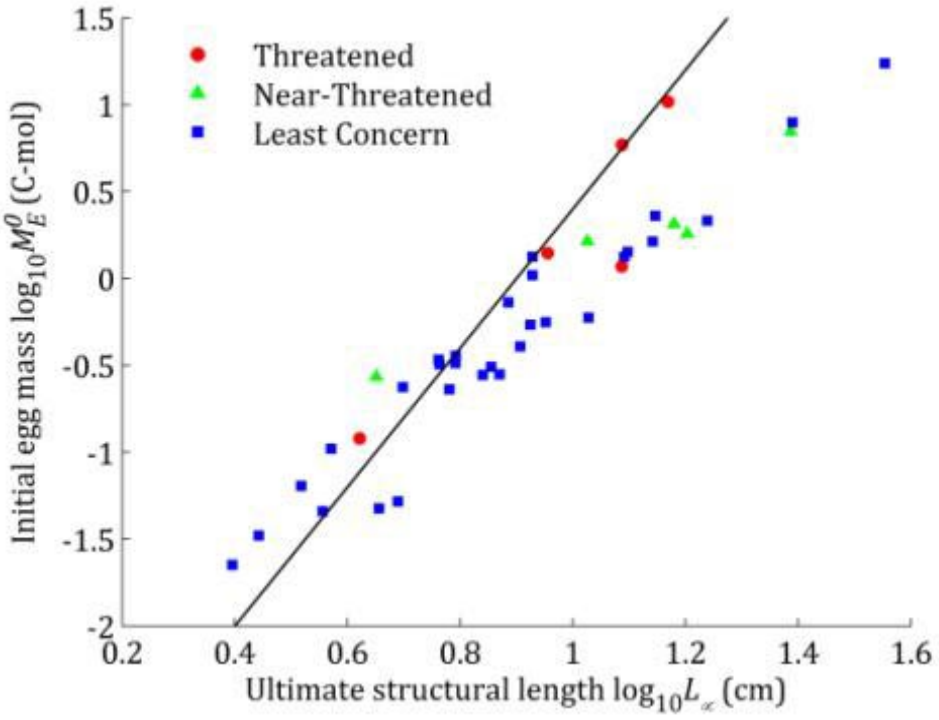

Figure 3.17 – Log-log plot of the initial egg mass (M_E^0, C-mol) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal.

3.3.3.8 Specific allocation to reproduction per maximum structural volume ($\dot{p}_R^m / L_m^3$, J d^{-1} cm^{-3})

The allocation to reproduction is expected to increase with L_m^3 and therefore the specific allocation to reproduction per maximum structural volume ($\dot{p}_R^m / L_m^3$, J d^{-1} cm^{-3}) is expected to be independent of L_∞. Our results differ from what is expected as we found a significant, yet moderate and negative correlation between $\dot{p}_R^m / L_m^3$ and L_∞ (Table 3.10). Our ninth and tenth hypotheses suggested that marine or pelagic and migratory species should exhibit lower values regarding the allocation of energy to reproduction. Our results confirm these expectations but the differences are not significant. The only significant difference observed is related to Nest type. Species that use closed nests allocate more energy to reproduction per volume than those that use open nests (Table 3.11). Nevertheless, L_∞ explains about 28% of the variation observed in $\dot{p}_R^m / L_m^3$ and the factor that explains a greater part of the remaining variation is the Superorder (Table 3.12) with the Palaeognathae exhibiting higher values than the Neognathae (Figure 3.18).

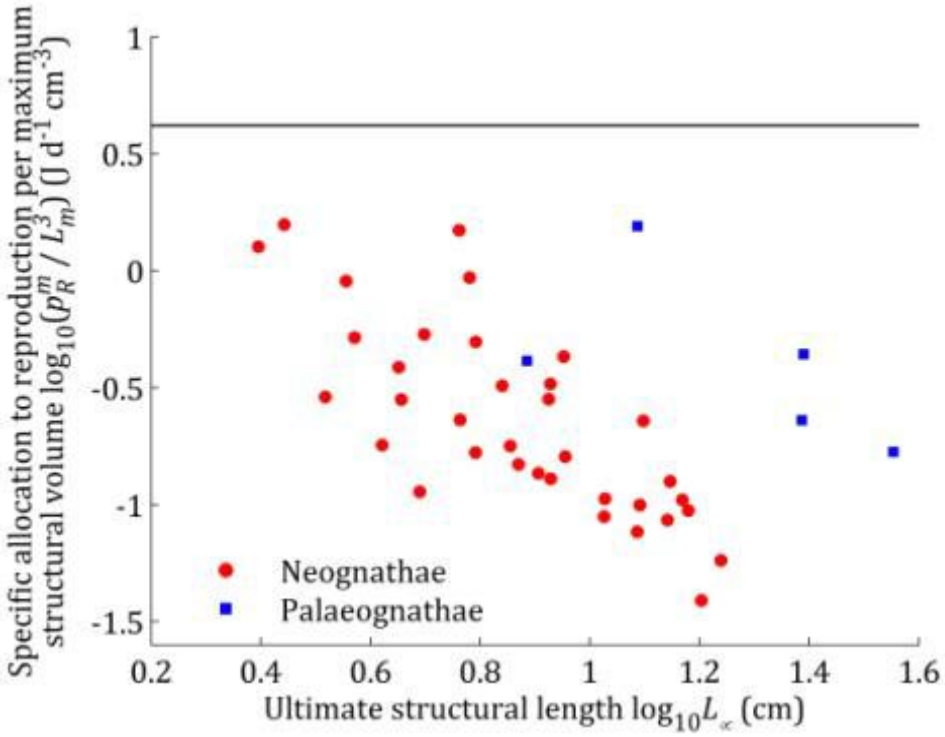

Figure 3.18 – Log-log plot of the specific allocation to reproduction per maximum structural volume ($\dot{p}_R^m / L_m^3$, J d^{-1} cm^{-3}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal.

3.3.3.9 Maturity maintenance at puberty per maximum structural volume ($\dot{p}_J^p / L_m^3$, J d^{-1} cm^{-3})

The maturity maintenance at puberty per maximum structural volume ($\dot{p}_J^p / L_m^3$, J d^{-1} cm^{-3}) is not expected to scale wito body size. However, we observed for this parameter a similar pattern to the one observed for $\dot{p}_R^m / L_m^3$. The maturity maintenance at puberty per maximum structural volume correlates significantly, yet moderately and negatively with L_∞ (Table 3.10). The only significant difference was also related to Nest type with the species that use closed nests allocating more energy to maintain maturity at puberty per volume, than those that use open nests (Table 3.11). The Nest type and Flight capacity are the two main factors describing the variation we observed in this parameter, followed by the effect of L_∞, but together these factors still just explain about 32% of the variation (Table 3.12). Bird species that are unable to fly exhibit higher values than the bird species that fly but this result is highly influenced by the Kagu and the North Island Brown Kiwi, which are flightless and that along with the Red Junglefowl (almost flightless) display the highest values of maturity maintenance at puberty per maximum structural volume (Figure 3.19).

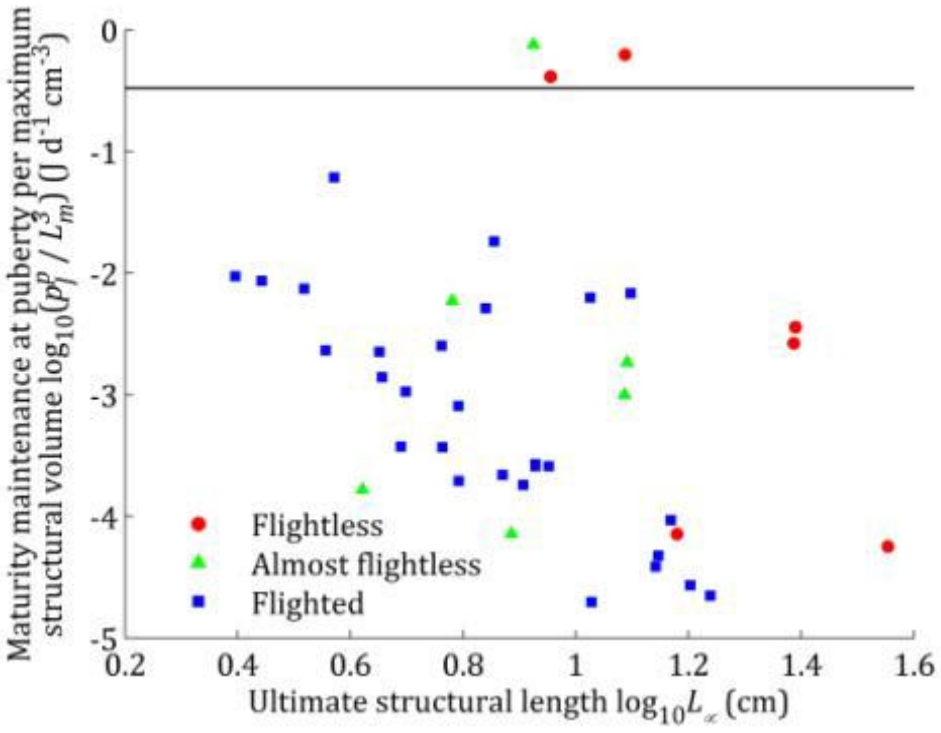

Figure 3.19 – Log-log plot of the maturity maintenance at puberty per maximum structural volume ($\dot{p}_J^p / L_m^3$, J d^{-1} cm^{-3}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal.

3.3.3.10 Dry mass-specific maturity at birth (hatching) ($\mu_H^b = E_H^b / M_V^b$, J mol^{-1})

The dry mass-specific maturity at birth (hatching) ($\mu_H^b = E_H^b / M_V^b$, J mol^{-1}) is not expected to scale with body size and our results are consistent with this observation. This property is not significantly correlated with L_∞ (Table 3.10). Most of the values are also below the expectation from the generalized animal, except for the case of the North Island Brown Kiwi, the most precocial species of our sample (Table 3.3) which stands out, just as it did for the low κ it displayed, this time exhibiting the highest value for μ_H^b among our collection of bird species. The lowest value is exhibited by the semi-altricial Adélie Penguin, a pelagic species that has one of the highest specific densities of dry structural mass (d_V^d = 0.5 g cm^{-3}) and therefore a higher amount of dry mass relative to its average body size. Significant differences were found for several factors.

Significant differences were observed regarding several factors. The Palaeognathae, polygamous, terrestrial, non-migratory and plantivore bird species invest more energy in maturation per C-mol of dry mass during the incubation period than the Neognathae, the monogamous, marine/pelagic, migratory and faunivore birds species. Those species that will involve a single progenitor during the nestling stage also exhibit significantly higher values than the ones that involve the pair of progenitors, which makes sense if we consider that the hatchlings of the former will hatch with a higher level of maturity than the hatchlings of the latter and therefore may require less amount of parental care (Table 3.11). In fact, Parental care is the most relevant factor explaining the variation in μ_H^b. Coupled with L_∞, differences regarding the Superorder and Flight capacity, about 64% of the variation is accounted for (Table 3.12) (Figure 3.20).

Considering that the typical interpretation of altriciality relates to higher levels of maturity being expressed in the hatchlings of bird species, it is also not surprising to observe that the precocial species of our sample exhibit higher values for this parameter than the altricial species. Despite the fact that this difference is not significant, future studies with a larger collection of bird species may provide better clues regarding the utility of this DEB property to assess the altricial-to-precocial spectrum.

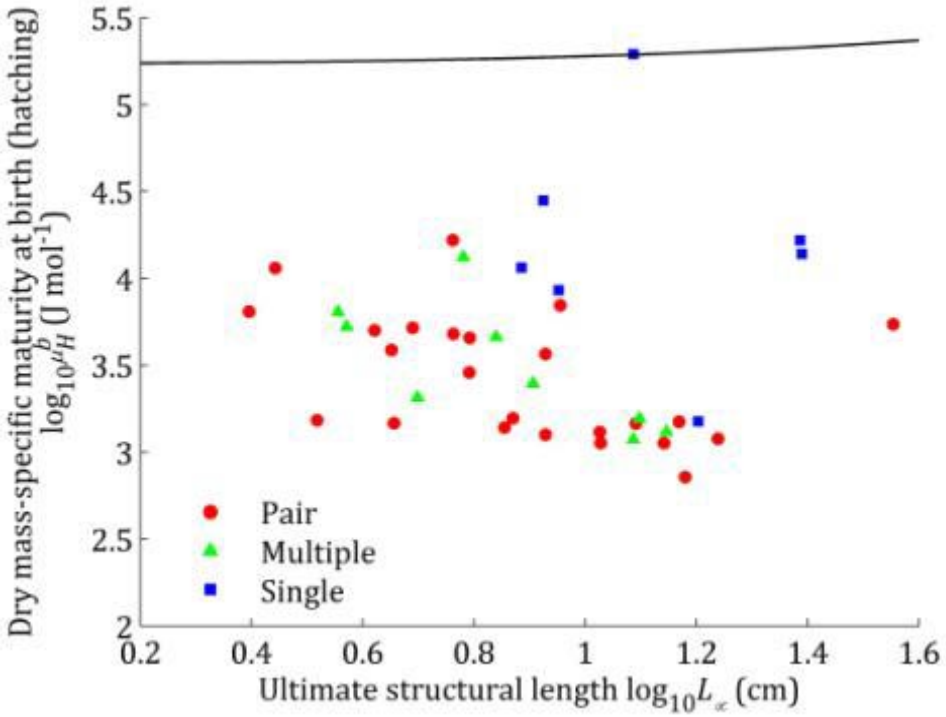

Figure 3.20 – Log-log plot of the dry mass-specific maturity at birth (hatching) (μ_H^b, J mol^{-1}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal.

3.3.3.11 Dry mass-specific maturity at fledging ($\mu_H^x = E_H^x / M_V^x$, J mol^{-1})

Just as with μ_H^b, the dry mass-specific maturity at fledging ($\mu_H^x = E_H^x / M_V^x$, J mol^{-1}) is not significantly correlated with L_∞ (Table 3.10). This is not surprising considering that there was no expectation for such a pattern to exist. Some values are positioned above and others below the expectations from the generalized animal. The highest value is once again exhibited by the North Island Brown Kiwi and the lowest value by the Adélie Penguin. However, the values are less scattered than those related to birth and no significant differences were found for any of the factors considered (Table 3.11) suggesting that this property is actually quite stable within our sample of bird species, i.e., despite the many differences in the range of species that constitute our sample, the amount of energy invested in maturation, up to the moment when nestlings fledge, per unit of dry mass is not so different. Fledglings are less different in terms of their relative maturity so the time spent in the nest and the parental care provided probably balance out the differences observed when they hatched. The most relevant factor explaining the scatter we observe in the estimated values for this parameter is the Superorder (Table 3.12) with the Palaeognathae exhibiting higher values than the Neognathae. Coupled with L_∞, about 30% of the scatter is described (Figure 3.21).

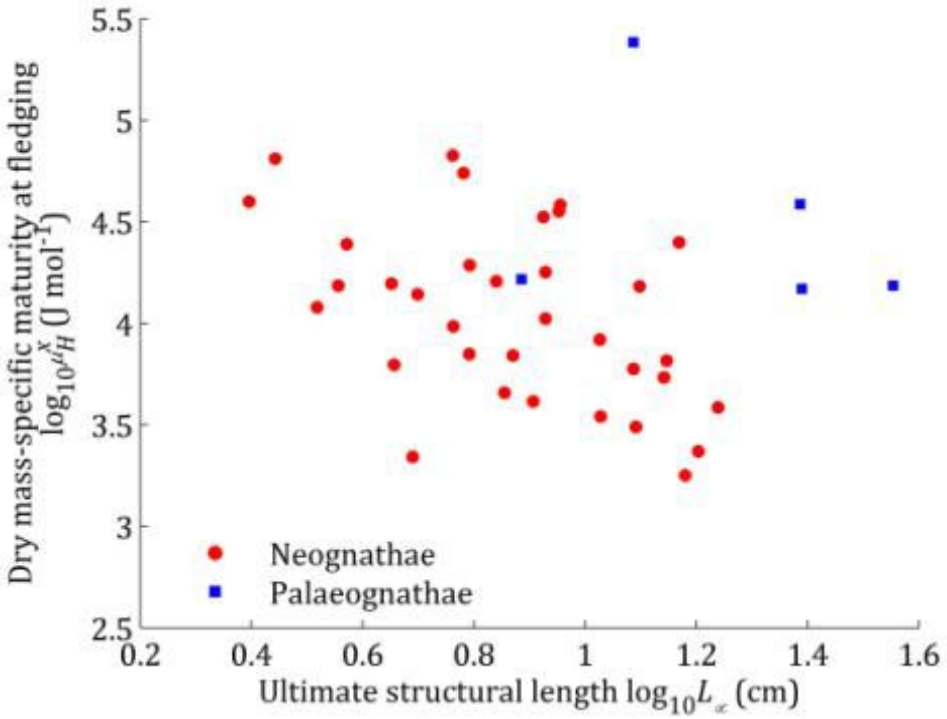

Figure 3.21 – Log-log plot of the dry mass-specific maturity at fledging (μ_H^x, J mol^{-1}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K.

3.3.3.12 Dry mass-specific maturity at puberty ($\mu_H^p = E_H^p / M_V^p$, J mol^{-1})

Just as with μ_H^b and μ_H^x, the dry mass-specific maturity at puberty ($\mu_H^p = E_H^p / M_V^p$, J mol^{-1}) is not expected to scale with body size and the values computed are indeed not significantly correlated with L_∞ (Table 3.10). Some values are positioned above and others below the expectations from the generalized animal. The highest value is exhibited by the Herring Gull, a species with an unusually long juvenile period (3 years) for its size. The third and sixth hypotheses of our study suggested that bird species with the capacity to fly and build nests in higher locations should reach sexual maturity sooner than those which are unable to fly and nest closer to the ground. We did not observe significant differences related to Flight or Nest level but we observed significantly higher values of μ_H^p in bird species that use closed nests and inhabit temperate regions (Table 3.11). The estimated values are quite scattered and every factor considered adds little to explain the variation with the Climate being the first, significant explainable variable (Table 3.12). Most of the scatter will probably change if more accurate data regarding the real onset of sexual maturity in birds becomes available (Figure 3.22).

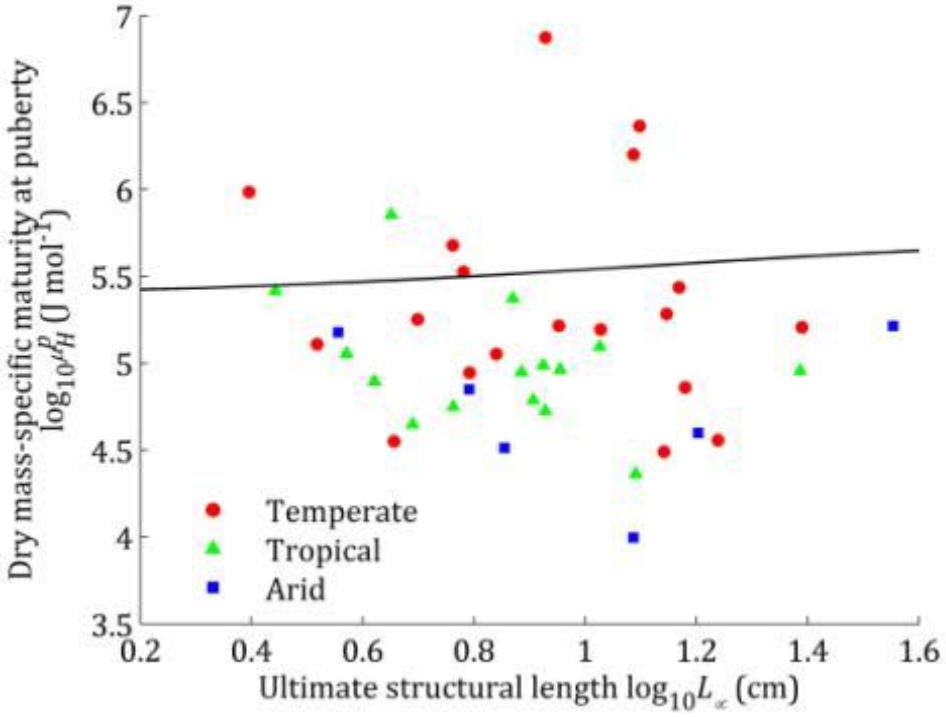

Figure 3.22 – Log-log plot of the dry mass-specific maturity at puberty (μ_H^p, J mol^{-1}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal.

3.3.3.13 Puberty/birth altriciality index (s^{pb}_H, -)

The puberty/birth altriciality index ($s^{pb}_H = E^p_H / E^b_H$, -) should provide an indication of the energy investment in maturation up to birth relative to the corresponding investment up to puberty. A higher value should illustrate a relatively low investment up to birth, which could be summarized as a higher degree of altriciality. This ratio is therefore not expected to scale with body size but we observed a significant, yet moderate, correlation with L_∞ (Table 3.10).

The semi-altricial European White Stork and the semi-precocial Herring Gull exhibit the highest ratio values within the group, but the reason lies particularly on the long juvenile periods of these two species (4 and 3 years, respectively) and the energy investments in maturity up to puberty (7.2×10^4 and 6.9×10^4 kJ, respectively) which stand out more comparing to the group median (8.8×10^2 kJ) than the investment in maturity up to birth (1.1 and 2.2 kJ, respectively) comparing to the corresponding group median (0.9 kJ).

The precocial North Island Brown Kiwi and the precocial Red Junglefowl exhibit the lowest ratio values but in these cases the reason may lie on the energy invested in maturity up to birth (5.8×10^2 and 7.4 kJ, respectively) which stands out more comparing to the group median, than the investment in maturity up to puberty (4.5×10^4 and 8.4×10^2 kJ, respectively) comparing to the corresponding group median.

This pattern is mostly explained by the higher correlation of E^p_H than of E^b_H with L_∞, i.e., the difference between larger birds and smaller ones, with regard to maturity, is bigger at puberty than at birth. However, the duration of the juvenile period is mostly based on observations regarding the age when the first successful reproductive event occurs. When considering species that reproduce for the first time much later than the completion of somatic growth, such as the European White Stork, than we may be overestimating the duration of the juvenile period as sexual maturity may have been reached much time before than the first successful reproductive occurrence. These overestimates will result in overestimated puberty/birth altriciality index results. When considering species that reproduce rather early, such as the Red Junglefowl, the low value we obtain through this index may constitute a more accurate indication of the species precociality. In any case the uncertainty regarding the data on puberty may decrease the reliability of the puberty/birth ratio as an indicator of altriciality.

Notwithstanding, significant differences were found between categories of birds according to several factors (Table 3.11). Marine and pelagic, flighted and migratory species were found to be more altricial than terrestrial, flightless and non-migratory species, respectively. We also observed lower values for altricial species than for precocial species. This result seems to be incoherent but it is easy explained by differences regarding E^p_H and not E^b_H.

The factor that explains a larger amount of the variation is the Migratory status (about 33%) (Table 3.12). Coupled with the Development type, about 45% of the variation is accounted for (Figure 3.23).

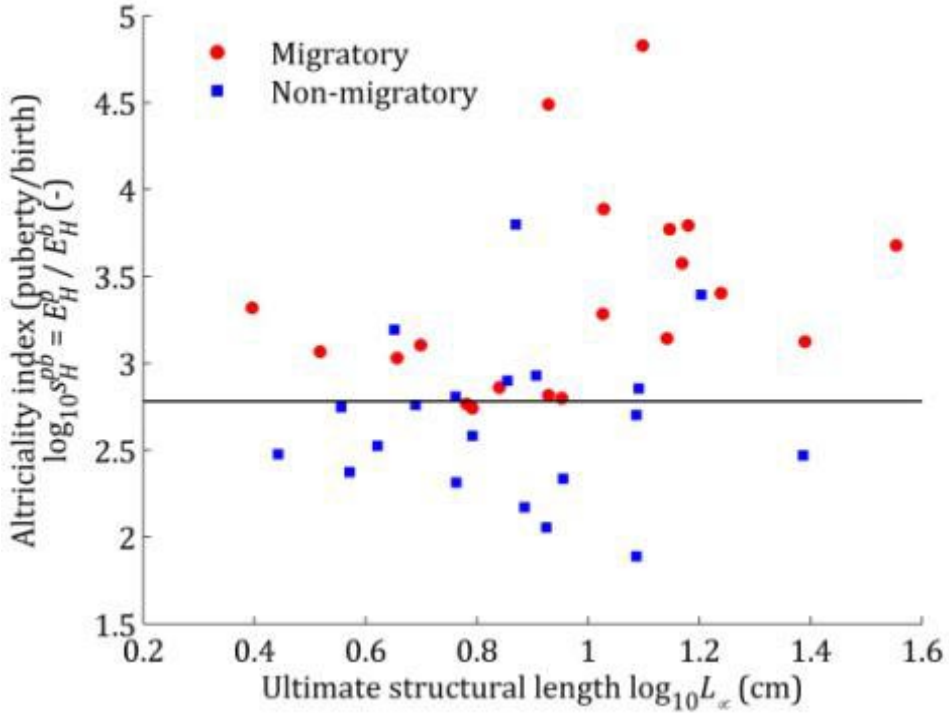

Figure 3.23 – Log-log plot of the puberty/birth altriciality index (s_H^{pb}, J mol^{-1}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K. The line represents the expected values according to the generalized animal.

3.3.3.14 Fledging/birth altriciality index (s^{xb}_H, -)

The fledging/birth altriciality index ($s^{xb}_H = E^x_H / E^b_H$, -) constitutes an alternative indicator of altriciality. As expected, there is no significant correlation between this parameter and L_∞ (Table 3.10). The highest values are exhibited by the semi-altricial European White Stork and the semi-precocial Wandering Albatross but the reason is once again mostly driven not by the energy invested in maturity up to birth but by the relatively high investment estimated to occur up to the fledging period. The lowest values are exhibited by the precocial North Island Brown Kiwi and the precocial Emu and in both these cases the results are not surprising considering that fledging is considered to occur soon after birth (particularly in the case of the Emu) and the thresholds are very close. Nevertheless, significant differences were found for several factors (Table 3.11). The Neognathae, migratory and faunivores present higher values than the Palaeognathae, non-migratory and plantivores bird species. Not surprisingly, some differences are related to the Mating system and Parental care. Species with higher values for this parameter, i.e., species that invest more energy in maturity during the nestling stage and up to fledging relative to the energy invested during incubation, are monogamous and it is usually the pair of progenitors or a group of helpers that take care of the nestling.

It is also possible to observe that altricial and semi-altricial species exhibit higher values for this parameter than semi-precocial and precocial bird species although the differences are not significant. Nevertheless, most of the variation is explained by Parental care, followed by the Migratory status (Figure 3.24). Despite the higher accuracy of fledging data, considering that one can actually observe the moment a bird fledges from the nest, compared to sexual maturity estimates, the fledging/birth ratio also seems to apply better as an indicator of precociality.

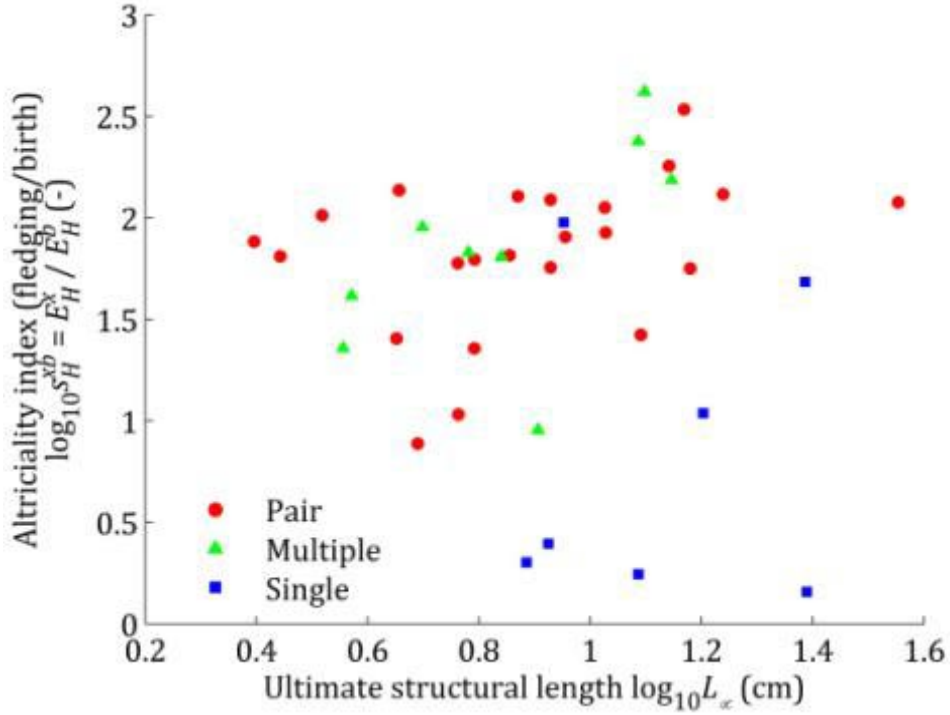

Figure 3.24 – Log-log plot of the fledging/birth altriciality index (s^{xb}_H, J mol^{-1}) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K.

3.3.3.15 Puberty/birth dry mass specific maturies ratio (μ_H^p / μ_H^b, -)

The puberty/birth dry mass specific maturies ratio (μ_H^p / μ_H^b, -) could also function as an alternative indicator of altriciality. This ratio is not expected to scale with body size and no correlation with L_∞ was observed (Table 3.10). Significant differences were observed regarding several categories but these were almost identical to those observed regarding the s_H^{pb} (Table 3.11). The most relevant factor explaining the distribution of values was the Migratory status, just as it was observed for the s_H^{pb} but the amount described is lower (27%). However, coupled with the Development type, about 51% of the variation is explained a slightly higher value than with the s_H^{pb} (Table 3.12) (Figure 3.25).

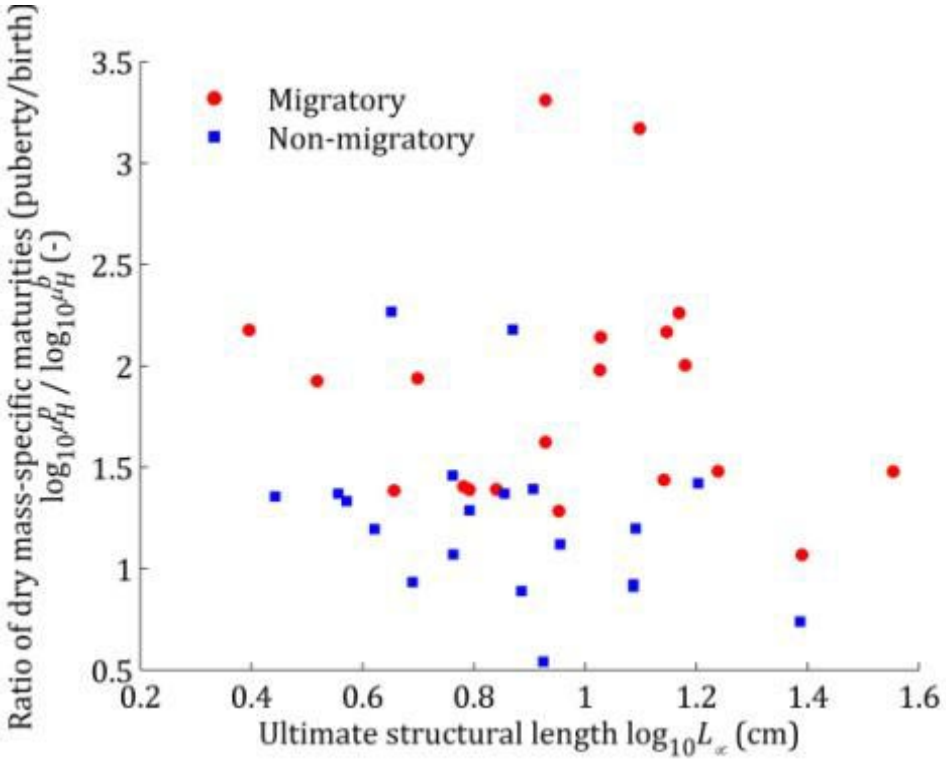

Figure 3.25 – Log-log plot of the puberty/birth dry mass-specific maturities ratio (μ_H^p / μ_H^b, -) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K.

3.3.3.16 Fledging /birth dry mass specific maturies ratio (μ_H^x / μ_H^b, -)

Just as with the previous ratio, the fledging/birth dry mass specific maturies ratio (μ_H^x / μ_H^b, -) could also function as an alternative indicator of altriciality. This ratio is not expected to scale with body size and no correlation with L_∞ was observed (Table 3.10). Also similar to what was observed with the previous ratio is the fact that the significant differences coincide with those observed regarding the s_H^{xb} (Table 3.11). The most significant factor describing the variation we observe in this ratio is the Mating system, which is different from what was observed regarding the s_H^{xb} (Parental care). However, the second most relevant – the Migratory status – coincides with the observations regarding the s_H^{xb} (Table 3.12).

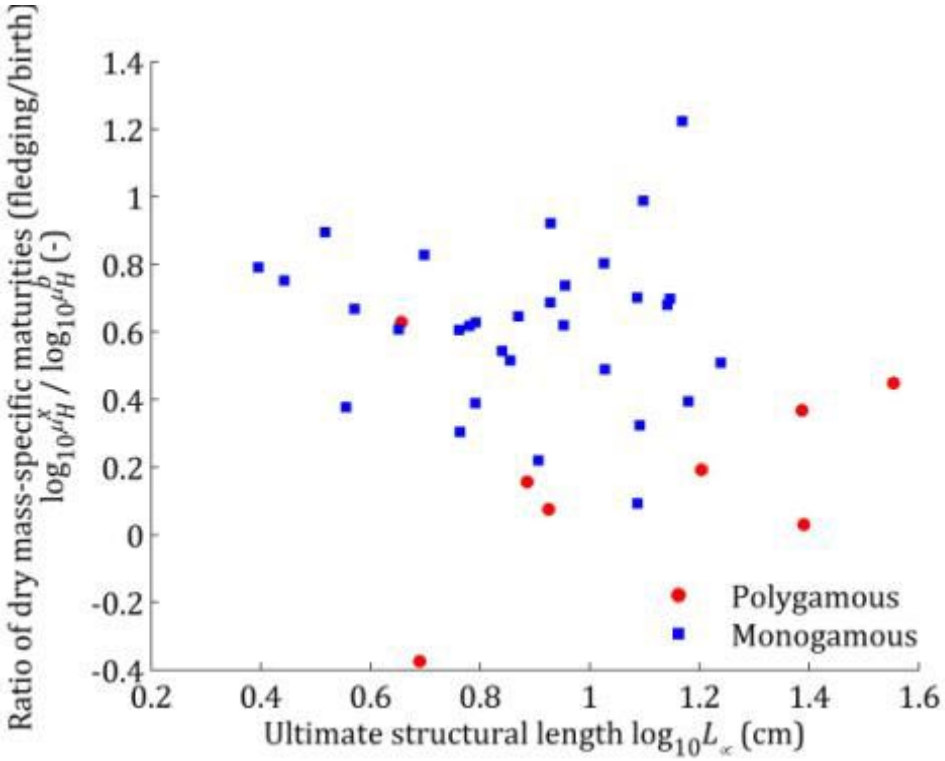

Figure 3.26 – Log-log plot of the fledging/birth dry mass-specific maturities ratio (μ_H^x / μ_H^b, -) as a function of the ultimate structural length (L_∞, cm) at the reference temperature of 293 K.

3.4 Discussion

3.4.1 Initial remarks

Several of the ecological factors considered for this study are significantly correlated with the ultimate structural body length L_∞ (Table 3.10), namely the Superorder, the Development type, the Flight capacity, the Nest level, the Nest type and the Foraging habitat. These correlations mean that, to a certain extent, the bird species are distributed among different categories – within those ecological factors – in such a way that larger birds are mostly concentrated in one or two categories and smaller birds in one or two other categories. However, although significant, these correlations are weak or moderate, leaving a considerable number of species distributed throughout the categories in such a way that is not correlated with body size. Nevertheless, considering that strictly based on DEB theory, some primary and compound DEB parameters are expected to scale with body size, then these correlations also mean that we should expect significant differences to emerge between categories of these ecological factors. For instance, the categories grouping larger bird species should exhibit higher assimilation rates, maturity thresholds, ageing acceleration rates, reserve capacities, fasting capacities, initial egg mass values and maximum wet weights per ultimate structural volume. They should also display lower von Bertalanffy growth rates and dry mass-specific respiration rates.

As it was previously reported for each analysed DEB parameter, our results generally confirm these expectations but a few exceptions need to be highlighted. One of those exceptions refers to the surface-specific assimilation rate ($\{\dot{p}_{Am}\}$, J d^{-1} cm^{-2}). This compound DEB parameter was expected to scale with L_∞ and it does correlate moderately with L_∞ (Table 3.10) but significant differences were only observed between marine/pelagic and terrestrial species and in the context of other ecological factors that are not correlated with body size, namely the Migratory status, the Climate and the Diet. The same observation can be made for the maximum reserve capacity ($[E_m]$, J cm^{-3}). This parameter is strongly correlated with L_∞ (Table 3.10) but differences are only related with the Mating system, the Nest level and the capacity to exhibit Torpor.

Nevertheless, for most DEB parameters that are expected to scale with body size, that expectation is met by our results and the ecological factors that are correlated with body size exhibit significant differences that need to be interpreted taking body size into account (Table 3.11). The Palaeognathae, precocial and flightless bird species as well as those that use open nests placed in low locations, exhibit higher cumulated energy investments in maturity, ageing acceleration rates and initial gg masses as well as lower growth and respiration rates than the Neognathae, altricial and flighted bird species of our sample that build closed nests and nest in high locations. Exceptions include Nest type and the Development type, for which not all of these differences are actually significant and the Foraging habitat, for which these differences are not present.

Considering the ecological factors that are not significantly correlated with L_∞ (Table 3.10), namely Migratory status, Climate, Mating system, Parental care, Diet and Torpor, the occurrence of significant differences, regarding the primary and compound DEB parameters that are expected to scale with body size, require explanations that are independent of body size and have an evolutionary meaning of their own. The same happens of course with the case of those differences observed for DEB parameters that are not expected to scale with body size, independently of the ecological factor in cause.

The multiple regression analysis allowed us to explore how different ecological factors could help to explain the variation we obtained in our estimations for the DEB parameters, beyond the effect of body size. By doing so we understood that a significant association between the scattered values of any DEB parameter and any particular ecological factor could provide valuable insights regarding: a) the evolutionary selective pressures that may have shaped this diversity and that may be constraining it; and b) how different behavioural strategies such as those related to the mating system or parental care, could have been driven by specific metabolic arrangements.

Our results allowed us to conclude the explaining power of body size for most of the DEB parameters and properties analysed. For 16 of these 26 DEB parameters and properties, the ultimate structural length, L_∞ was the first or second most significant variable and for 10 of them it was the main explaining factor (Table 3.12). Considering at least four explaining variables, then the ultimate structural length is included as an explaining variable for 20 of the DEB parameters and properties. With these four variables an average of 62% of the variation observed was explained, ranging from the 35% (μ_H^p) to 94% (M_E^0). The majority of the scatter observed regarding the values we estimated for the DEB parameters and properties detailed in this study is therefore potentially explained by the set of ecological factors and corresponding categories we defined. Among the ecological factors considered for this study, the Development type, the Migratory status and the Superorder were the three most frequently significant factors, helping to describe the variation of estimated DEB parameters' values, beyond the expected effect of body size. However, there are aspects worth discussing for all the other factors too which are detailed in the following section.

3.4.2 Ecological characterization

3.4.2.1 Superorder

The first hypothesis of our study suggested that differences between the Palaeognathae and the Neognathae should reflect the effect of body size. Our sample of Palaeognathae species does have a significantly higher average body mass (U (38) = 26, n_1 =35 n_2 = 5, p = 1.27 × 10^{-2}) and body length (U (38) = 33, n_1 =35 n_2 = 5, p = 2.72 × 10^{-2}) than the Neognathae, and the differences were expected for all the DEB parameters that scale with body size were confirmed, except for the cases of $\{\dot{p}_{Am}\}$ and $[E_m]$ (Table 3.11). We also observed that the Neognathae have significantly higher κ values than the Palaeognathae. Considering the low coefficient of variation of κ this suggests that the evolution of Neognathae went towards a higher investment in somatic growth and maintenance, i.e., a down-regulation of reproduction effort. Supporting this observation are the higher values of $\dot{p}_R^m$ / L_m^3 observed for the Palaeognathae. The significantly higher values observed for the Neognathae regarding $\dot{v}$, $[\dot{p}_M]$ (and consequently $\dot{k}_M$), $\dot{r}_B$ and -J_O / W_d (Table 3.11) suggest that the higher growth and respiration rates in this group co-evolved with necessarily higher reserve mobilisation rates and somatic maintenance requirements. Evolving in this direction – which may also related to the emergence of flight – constrained the Neognathae reserve and fasting capacities, which according to our results are lower than what we observe in the Palaeognathae species, confirming in a quantified and metabolically explicit manner the previous expectations suggested in the literature by Konarzewski et al. (1998).

Our results also suggest that contrary to the Palaeognathae, the Neognathae adjust very well to the recently proposed waste-to-hurry hypothesis, according to which species consume more resources in order to remain small, grow fast, and respond quickly to temporal and local food

abundance (Kooijman, 2013). These results may also be related to the most frequent development types in each Superorder.

3.4.2.2 Development type

Our results confirm the expectation presented by Konarzewski *et al.* (1998) that differences observed in the altricial-to-precocial spectrum of development types should find expression in the DEB parameters themselves.

The second hypothesis of our study, based on observations obtained from a variety of different studies, suggested that altricial bird species should exhibit higher growth rates and smaller eggs than precocial species. Our results include significant differences between altricial and precocial species regarding $\dot{r}_B$ that confirm the first expectation. According to our results altricial and semi-altricial species also have significantly higher values of $\dot{v}$, $[\dot{p}_M]$, $\dot{r}_B$ and $-J_O / W_d$ than precocial species and altricial species have significantly lower fasting capacities than precocial species (the reserve capacities are also lower but not significantly) (Table 3.11). These results are similar to those observed when comparing the Palaeognathae and Neognathae and to a certain point the fact that all the Palaeognathae species are precocial contributes to that. Nevertheless, these patterns also suggest that within the Neognathae, the adoption of altricial strategies is also consistent with the waste-to-hurry hypothesis. Once again, the higher $\dot{v}$ values, constraining $[E_m]$, may have co-evolved with the emergence of flight.

The differences regarding the estimated von Bertalanffy growth rates are very clear and progressive even when we plot the average values according to each type of the eight categories of development pattern with which we initially characterized the species. The co-evolution of growth rates towards higher values in progressively altricial development patterns was clearly supported by increasing somatic maintenance costs and reserve mobilisation rates (Figure 3.27).

Concerning the eggs, we observed lower values of M_E^0 for the altricial species despite the fact that the difference was not yet significant. As Dyke & Kaiser (2010) observed, the evolution of unrestricted egg size may have stimulated the diversification of birds. With relatively larger eggs, smaller birds may have been selectively pressured to evolve higher growth rates, under different environmental factors. Reserve mobilisation rates provided the necessary plasticity. Smaller birds, the evolution of flight and more dynamic lifestyles and diets (Konarzewski et al., 1989) may also explain the significantly lower fasting capacities we observed in altricial species.

The typical interpretation of altriciality associates the phenotype of altricial species to a somewhat less mature state mostly due to the absence of locomotion, feathers and other traits that are present in the phenotype of precocial hatchlings, as well as due to the intensive parental care that altricial species require. However, different tissues have been studied in both kinds of birds and if on the one hand muscles for locomotion purposes are much more developed in precocial birds when they hatch (Hohtola and Visser, 1998), on the other hand the organs of the digestive system are much more developed in altricial species possibly to support the high post-hatching growth rates (Klasing, 1999). These observations suggest the possibility that, on average and considering the whole organism, both types of development could share a similar overall complexity which through DEB theory would correspond to similar investments in maturation per unit of dry mass.

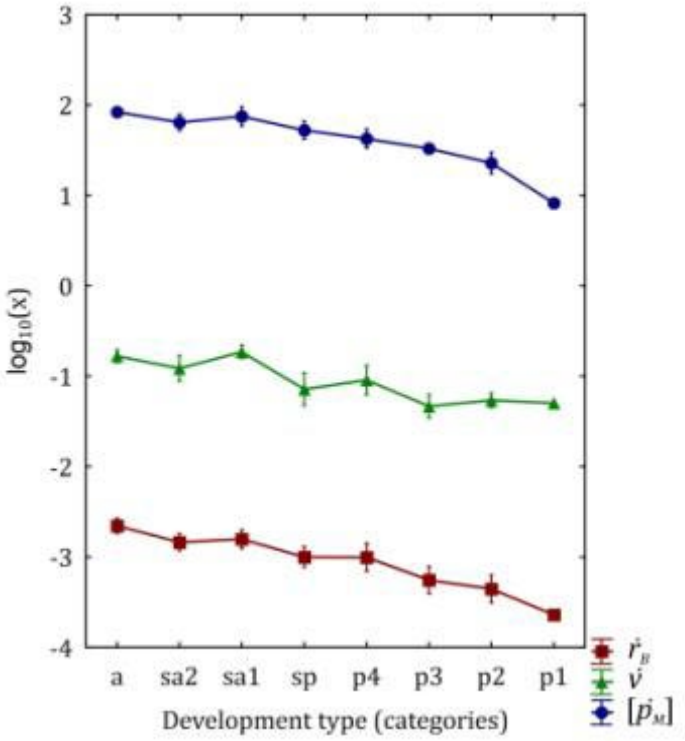

Figure 3.27 – Average von Bertalanffy growth rate ($\dot{r}_B$, d^{-1}), energy conductance ($\dot{v}$, cm d^{-1}) and volume-specific somatic maintenance rate ($[\dot{p}_M]$, J d^{-1} cm^{-3}) at the reference temperature of 293 K, for each type of development pattern. Abbreviations for the categories are as follow: a – altricial; sa2 – semi-altricial 2; sa1 – semi-altricial 1; sp – semi-precocial; p4 – precocial 4; p3 – precocial 3; p2 – precocial 2; p1 – precocial 1.

We observed that precocial species exhibit significantly higher values of E_H^b than altricial species, investing higher amounts of energy into maturation during the embryonic stage. However, we also observed that both the Development type, as a factor, and the E_H^b, as a parameter that scales with L_∞^3, are significantly correlated with L_∞ (Table 3.10), which means that these differences are basically driven by differences in size between altricial and precocial species. In fact, significant differences were also observed regarding E_H^p (Table 3.11).

Nevertheless, we also observed that precocial species exhibit higher values of the dry mass-specific maturity at birth, μ_H^b (J mol^{-1}) than altricial species, i.e., they invest more energy into maturation per unit of dry mass. This difference is almost significant (p = 0.055). If we consider the relative investment in maturation as an indicator of complexity, then these results support the thesis of higher complexity in precocial birds.

At this point it is worth to compare the average values of μ_H^b with those of the two altriciality index alternatives (s^{pb}_H and s^{xb}_H) as well as with the average values of the ratios (μ_H^p / μ_H^b and μ_H^x / μ_H^b), for each of the eight categories in the altricial-to-precocial spectrum presented by Ehrlich et al. (1988), namely: altricial; semi-altricial 2; semi-altricial 1; semi-precocial; precocial 4; precocial 3; precocial 2 and precocial 1. All the options seem to perform reasonably well as indicators of the degree of altriciality (or precociality) in bird species but the slopes resulting from the dry-mass specific maturity ratios are not as accentuated as those regarding both types of the altriciality index used. The puberty/birth altriciality index seems to register larger differences between categories sa1 and sa2 than the fledging/birth altriciality index. On the other hand, the former type registers smoother differences between the p2 and p3 categories than the latter. Overall, the average differences regarding μ_H^b seem to be smoother and more

adequate to function as an indicator of the more altricial or precocial nature of bird species (Figure 3.28).

It is now clear that through the application of DEB theory, the altricial-to-precocial spectrum may be assessed based on simple data such as the input data that was used to estimate the DEB parameters for the sample of bird species considered in this study. The difficulty of assessing to which degree a species is positioned in this spectrum through experimentation and the use of expensive and invasive techniques may now be overcome through the simple application of DEB theory.

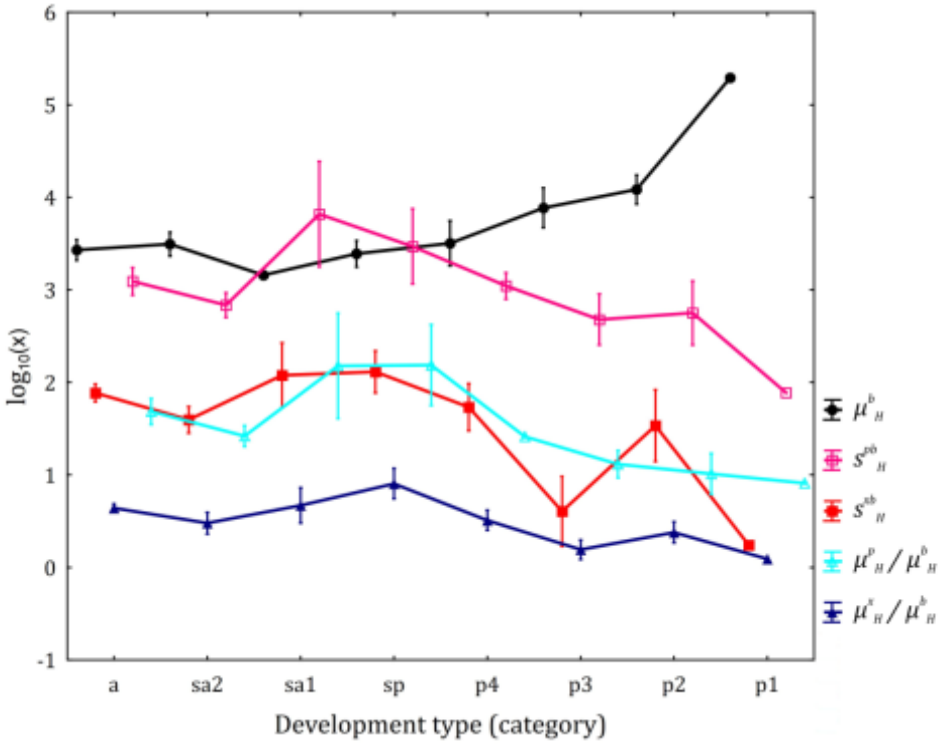

Figure 3.28 – Estimates regarding the altricial-to-precocial spectrum of development patterns, at the reference temperature of 293 K. The parameter abbreviations and their corresponding names are the following: μ_H^b – dry mass-specific maturity at birth (hatching) ($\mu_H^b = E_H^b / M_V^b$) (J mol^{-1}); s^{pb}_H – puberty/birth altriciality index (-); s^{xb}_H – fledging/birth altriciality index (-); μ_H^p / μ_H^b – puberty/birth dry mass specific maturies ratio (-); μ_H^x / μ_H^b – fledging/birth dry mass specific maturies ratio (-). Abbreviations for the categories are as follow: a – altricial; sa2 – semi-altricial 2; sa1 – semi-altricial 1; sp – semi-precocial; p4 – precocial 4; p3 – precocial 3; p2 – precocial 2; p1 – precocial 1.

3.4.2.3 Flight

The flying species of our sample are significantly shorter in length ($H(2) = 6.28$, $N = 40$, $p = 4.32 \times 10^{-2}$) and lighter in wet mass as hatchlings ($H(2) = 10.89$, $N = 40$, $p = 4.3 \times 10^{-3}$) and adults ($H(2) = 9.17$, $N = 40$, $p = 1.02 \times 10^{-2}$) than flightless species. Therefore, it was not surprising that every difference between flighted and flightless bird species regarding DEB parameters that are expected to scale with body size, including M_E^0 for examples, is significantly confirmed with our results. The exceptions are the $\{\dot{p}_{Am}\}$ and $[E_m]$. Bird species that are unable to fly have higher reserve capacity and assimilation rates but the differences are not significant.

Our third hypothesis suggested differences regarding $[\dot{p}_M]$, $\dot{r}_B$ and E_H^p, and all of them were also confirmed. Also as expected, the observations previously made regarding locomotion costs and their associated demands such as the capacity to mobilise reserve quickly and develop large pectoral muscles and heart masses, apply to birds when we consider flight. According to our results, flying birds exhibit higher $\dot{v}$, $[\dot{p}_M]$, $\dot{r}_B$ and $-J_O / W_d$ than birds that are almost flightless or unable to fly, although for $\dot{v}$ the difference is only significant between the first and the second categories due to the larger variation observed in flightless birds (Table 3.11). Notwithstanding, the difference is very clear and logical considering that in DEB theory locomotion costs are included in $[\dot{p}_M]$. Higher $\dot{v}$ and $[\dot{p}_M]$ values in flighted, smaller birds also constrained the fasting capacity of these species which exhibit significantly lower values for this parameter than flightless bird species do.

The association of higher $\dot{v}$, $[\dot{p}_M]$, $\dot{r}_B$ and $-J_O / W_d$ values suggests once again the waste-to-hurry hypothesis as we have concluded when considering the Superorder and the development of altriciality. Chinsamy & Elzanowski (2001) concluded that primitive birds may have been precocious fliers and found evidence for an early postnatal reduction of growth rates in two lineages of flying basal birds. Our results suggest that the evolution of altriciality in flying birds may have proceeded through the co-evolution of metabolic processes that are now expressed by DEB parameters.

Concerning maturity, we observed significantly lower maturity thresholds for hatching, fledging and puberty in flying birds than in flightless birds. Coupled with the smaller size, this is once again evidence of evolution towards a quicker pattern of development in flying birds (potentially driven by environmental factors such as predation) or of an optimization process regarding the relative investment in maturity, its maintenance and ultimately reproduction itself.

3.4.2.4 Mating system

Confirming the observations of Orians (1969), the Mating system and Development type are significantly, yet moderately, correlated ($r(38) = 0.46$, $p = 2.67 \times 10^{-3}$) and the parallelism regarding the differences observed between monogamous and polygamous species and those observed between altricial and precocial species is not surprising. Monogamous species exhibit significantly higher values of $\dot{v}$, $[\dot{p}_M]$, $\dot{r}_B$ and $-J_O / W_d$ than polygamous species (Table 3.11). Our results also confirm the expectations of Royle et al. (1999) which served the basis for our fourth hypothesis, with monogamous species exhibiting significantly higher $\dot{r}_B$ values than polygamous species. The significantly higher values of $[E_m]$ of polygamous species are probably a consequence of the particular representativeness that the ratites have in this category. This also explains why the polygamous species in our sample also exhibited significantly higher t_s and W_w^m / L_∞^3 values than the monogamous species.

Our results suggest that monogamy in birds may have co-evolved with the evolution of altricial strategies, the adoption of higher postnatal growth rates and their associated higher reserve mobilisation rates and somatic maintenance costs. Altricial birds may require dedicated progenitors and monogamy may increase the likelihood of both progenitors participating in the parental care of the hatchling.

3.4.2.5 Parental care

We observed significantly lower values of κ in species in which the hatchling is cared for by a single progenitor. The same difference was observed regarding $\dot{v}$, $[\dot{p}_M]$, $\dot{r}_B$ and $-J_O / W_d$ (Table

3.11), confirming our fifth hypothesis. With significantly lower reserve mobilisation rates, the significant difference observed regarding the fasting capacity is not surprising, considering that those birds are able to maintain larger amounts of reserve available. These differences may reflect to which degree a higher investment in somatic growth and maintenance as well as in higher reserve turnover rates may have co-evolved with reproductive systems through which parental care is provided by two or more individuals. We also observed significant differences regarding μ_H^b. The hatchlings with lower dry mass-specific maturity at birth (i.e., according to our results on Development type, mostly altricial species) seem to require parental care from more than just one progenitor. The strategies related to parental care may have evolved as behavioural adaptations to relatively low maturity levels in hatchlings in many bird species. On the other hand, Parental care is significantly, yet moderately correlated with three other factors: Mating system ($r(38) = 0.53$, $p = 4.58 \times 10^{-4}$), Superorder ($r(38) = 0.5$, $p = 9.99 \times 10^{-4}$) and Nest level ($r(38) = 0.47$, $p = 2.1 \times 10^{-3}$). There is also a significant but weak correlation with Development type ($r(38) = 0.34$, $p = 3.1 \times 10^{-2}$) and therefore these differences may also be related to the fact that most of the bird species in our sample that rely on parental care from a single parent are also polygamous, precocial and belong to the Palaeognathae. We did not observe any significant difference between species that rely on parental care provided by both progenitors and those that rely on multiple helpers for any of the parameters which reinforces the probable exogenous nature of those factors driving the evolution of cooperative breeding in birds.

3.4.2.6 Nest level

We observed several significant differences between species that build their nests in high locations and those that build their nests in low locations. The former have significantly higher values of $\dot{v}$, $[\dot{p}_M]$, $\dot{r}_B$ and $-J_O / W_d$, than the latter (Table 3.11), confirming our sixth hypothesis. Once again, as consequences from these combinations of traits, species that build their nests in high locations also exhibit significantly lower $[E_m]$ and t_s values than those that nest in low locations. Appropriately, we also observed that species nesting in higher locations lay eggs with significantly lower mass (i.e., significantly lower M_E^0 values). Birds that nest in higher locations are also significantly smaller if we compare body mass at birth ($U = 74$, $n_1 = 20$, $n_2 = 20$, $p = 6.87 \times 10^{-4}$), adult body mass ($U = 82$, $n_1 = 20$, $n_2 = 20$, $p = 1.48 \times 10^{-3}$) or adult body length ($U = 107.5$, $n_1 = 20$, $n_2 = 20$, $p = 1.28 \times 10^{-2}$) than those that nest in low locations, which is aligned with the miniaturization trend that has recently been suggested for avian evolution by Lee *et al.* (2014). Besides being smaller, they are also relatively ligher, displaying significantly lower W_w^m / L_∞^3 values. We observed significantly lower energy values for all three maturity thresholds: hatching, fledging and sexual maturity in those species that nest in high locations but these are not surprising considering the fact that they scale with body size.

Whether the higher growth and reserve mobilisation rates as well as somatic maintenance costs we observed in species that build nests in high locations resulted from higher levels of predation pressure that occur in those environments, as Martin (1995) suggested, or exclusively as consequence of smaller body sizes is yet to be determined. Notwithstanding, the decrease in the amount of energy invested in all of the three maturity thresholds considered are possibly also a result of a shift in reproductive strategies that included the transition from precociality to altriciality.

3.4.2.7 Nest type

According to our results, bird species that use open nests have significantly lower values of $[\dot{p}_M]$ than those that use closed nests (Table 3.11). The species that use closed nests in our

sample are significantly smaller than those that use open nests if we compare body mass at birth (U = 72.5, n_1 = 29, n_2 = 11, p = 8.79 × 10^{-3}), adult body mass (U = 64, n_1 = 29, n_2 = 11, p = 4 × 10^{-3}) or adult body length (U = 77.5, n_1 = 29, n_2 = 11, p = 1.36 × 10^{-2}) and therefore the association between closed nest building, thermoregulation and body size, as suggested by Dyke & Kaiser (2010) is worth exploring in future studies. The species also lay significantly smaller eggs (i.e., lower M_E^0 values).

Contrary to what our seventh hypothesis suggested, we did not observe any significant difference regarding the growth rate but there is a significant, yet moderate correlation between the factors Nest type and Development type (r(38) = 0.4, p = 1.08 × 10^{-2}), probably influenced by the fact that several of the large, precocial birds use open nests but grow slowly as they are not as threatened by predators as those smaller, altricial birds that also use open nests.

Of particular evolutionary interest are the differences we observed regarding $\dot{p}_R^m$ / L_m^3 and $\dot{p}_J^p$ / L_m^3. Bird species allocating significantly higher amounts of energy to reproduction and maturity maintenance per volume use closed nests. On the one hand, this nesting strategy may just be another behavioural adaptation that co-evolved in terrestrial, altricial bird species that nest in high locations (these factors are moderately correlated) as a natural consequence of smaller birds exploring new arboreal niches (this factor is also moderately correlated with body size) (Table 3.10). On the other hand, it highlights the possible and important co-evolution between the miniaturization trend suggested by Lee *et al.* (2014) and life history strategies that may be prioritizing higher reproduction rates. On other very relevant conclusion may be the association of higher maturity levels (and corresponding maintenance) with higher reproductive effort.

3.4.2.8 Torpor

In the sample of species considered for this study, only the Common Swift, Tawny Frogmouth and the Blue-naped Mousebird are known to exhibit torpor. This small sample size increases the error but nevertheless we did not observe any significant correlation between Torpor and any other factor and observed a few significant differences. The group joining the three species that exhibit torpor have significantly higher values of $\dot{v}$, [$\dot{p}_M$], $\dot{r}_B$ and -J_O / W_d, than the rest of the species. They also exhibit significantly lower [E_m] and t_s values. Finally, according to our results, species that exhibit torpor also require significantly less energy to reach the maturity thresholds of hatching, fledging and puberty (Table 3.11). These differences confirm our eighth hypothesis but they may also be associated to the pattern observed for smaller, altricial birds that fly and nest in high locations. In fact, the three species that exhibit torpor, as a group, are significantly smaller than the rest of the species, if we compare body mass at birth (U = 14, n_1 = 37, n_2 = 3, p = 3.53 × 10^{-2}) or adult body length (U = 15, n_1 = 37, n_2 = 3, p = 4 × 10^{-2}) as well as relatively lighter (i.e., lower W_w^m / L_∞^3 values). The differences in adult body mass are almost significant as well. This association to body size is consistent with the previous studies referred. The significant differences regarding somatic maintenance costs may help to explain previous observations regarding higher basal metabolic rates in birds exhibiting torpor (McNab, 2012). However, the origin of these differences may be interconnected with the evolution of other life history traits associated with smaller sizes and a more active lifestyle. In fact, several authors have underlined the possible plesiomorphic nature of torpor (Geiser, 2008, 1998, 1988; Grigg, 2004; Grigg et al., 2004). Heterothermy would then actually be an ancestral trait that some groups would have retained, associated with specific life-histories.

3.4.2.9 Foraging habitat

We observed that despite a generally high κ value considering the whole sample of species, the marine or pelagic species of this group have a significantly higher κ and (almost significantly) lower $\dot{p}_R^m$ / L_m^3 than the ones that inhabit and forage terrestrial habitats, confirming the expectations of our ninth hypothesis (Table 3.11). Higher κ values have been described as corresponding to the down-regulation of reproduction (Kooijman and Lika, 2014b) and the lower allocation of energy to reproduction offers a metabolic explanation for the previous observations regarding the lower productivity of marine bird species (Dobson, 2012; Sibly et al., 2012). We also observed that at the reference temperature, marine or pelagic species have significantly higher $\dot{k}_J$ than terrestrial species and significantly lower $\{\dot{p}_{Am}\}$. The higher maturity maintenance rate coefficient is related to the high sexual maturity thresholds that we observe in birds such as the Wandering Albatross (first reproduction usually 6 years after hatching), the European Herring Gull and the Adélie Penguin (both usually reproducing for the first time 3 years after hatching). The differences observed regarding a higher surface-specific assimilation rate in marine or pelagic birds may result not just from habitat or diet particularities but also from their migratory lifestyles. Some of the terrestrial species in our sample are migratory and others are not but all the marine or pelagic species are indeed migratory. In fact, there is a significantly moderate correlation between the habitat and migratory factors ($r(38) = 0.61$, $p = 3.1 \times 10^{-5}$). On the other hand, marine or pelagic species often have extremely intense lifestyles as far as the effort in locomotion goes. The Wandering Albatross, for instance, is estimated to travel up to 8.5 million km during a 50 year lifetime (Weimerskirch et al., 2014). Previous studies have also estimated higher resting and basal metabolic rates in marine species when compared to terrestrial species (Bennett and Harvey, 1987; Nagy, 1987), which is consistent with our results.

3.4.2.10 Migratory status

The Migratory status was one of the three most relevant ecological factors for explaining the diversity of values observed for several primary and compound DEB parameters. According to our results, migratory species have significantly higher values for κ than non-migratory species (Table 3.11). This higher investment in somatic growth and maintenance supports previous observations regarding the particular demands that the migratory behaviour has on the physiognomy of birds and confirms our tenth hypothesis.

We also observed that migratory species exhibit significantly higher values for $\dot{v}$ and $\{\dot{p}_{Am}\}$ than non-migratory species. The ability to mobilise reserve at a significantly higher rate is once again supporting the observations regarding the demands of migratory flight (Hedenström, 1993; McWilliams et al., 2004) and the capacity for a significantly higher surface-specific assimilation rate in migratory birds also supports the observations detailed in many studies regarding food assimilation efficiency. In fact the increase of hyperphagia before migration has been characterized as essential for fat deposition but unable to account for the complete pre-migratory mass gain observed in sparrows which has also been attributed to an increase in assimilation efficiency (Bairlein and Gwinner, 1994).

Another significant difference between migratory and non-migratory species regards maturity. Migratory species hatch with significantly lower μ_H^b values (i.e., they are intrinsically altricial) and take significantly longer periods to achieve sexual maturity (U (38) = 123.5, n_1 =20 n_2 = 20, $p = 3.64 \times 10^{-2}$) and according to our results invest significantly higher amounts of energy to reach this threshold. However, we also observed that migratory species have significantly lower $\dot{k}_J$. As stated before, migratory birds, particularly those that perform long distance

migrations, have been previously characterized as having higher basal metabolic rates due to high maximum fuel deposition rates and the metabolic activity of food-processing organs or locomotion activity and respective elevated maintenance costs (Jetz et al., 2008; Lindström and Kvist, 1995), to their predominantly cold high-latitude breeding areas or as a result of measurements taken in different moments and circumstances (Jetz et al., 2008). The data we used to estimate our DEB parameters are of an ecological nature and consist mostly of average values obtained through observation (e.g., incubation duration) and weighting. No energetic measurements were required, reducing the risk of error from measurements taken in different circumstances and/or through different methods (e.g., respiration chambers, isotope administration, etc). It is also interesting to note that according to our results the differences between migratory and non-migratory species regarding somatic maintenance costs are not significant. This observation complements the lower maturity maintenance rate coefficient we observed and may reflect the energy optimization suggested to have occurred in migratory birds (Alerstam and Lindström, 1990; Alerstam, 2011; Lindström and Kvist, 1995).

3.4.2.11 Diet

We have only considered two categories regarding diet, essentially separating species that mostly consume material of vegetal origin ("plantivores") from those that mostly consume material of animal origin ("faunivores") and included the omnivores in the first category despite their intermediate basal metabolic rates (McNab, 2009) and the intermediate mean metabolizable energy content of the omnivorous diet (Nagy, 1987). Nevertheless, some significant differences were observed between the two groups (Table 3.11) including the fact that faunivores have a significantly higher κ than plantivores. This higher investment in growth and somatic maintenance, confirming our eleventh hypothesis, may be related to the anatomical implications of the diet itself as they are described by the continuous distribution of digestive-tract morphologies in birds (Klasing, 1999). We also observed significantly higher $\dot{v}$, $[\dot{p}_M]$ and $\{\dot{p}_{Am}\}$ values in faunivores. These results are consistent with expectations based on the observations by Kirkwood (1983) and Karasov (1990) regarding the existence of upper limits to food intake resulting from assimilation and metabolisation constraints and digestive tracts' size differences between faunivores and plantivores. Noteworthy is also the fact that bird species with significantly lower μ_H^b values seem to be faunivores. This may reflect another behavioural adaptation that co-evolved with altriciality, whereby densely energetic food is important for quick post-hatching development and that may be well illustrated through the adoption of insectivorous diets by many altricial bird species.

As referred before, according to DEB theory, locomotion costs are included in $[\dot{p}_M]$ (Kooijman, 2010a). The higher $\dot{v}$ and $[\dot{p}_M]$ values we observed in faunivores, further confirming our eleventh hypothesis, may not just be related to those higher locomotion costs, previously described by Schleucher (2002), Klasing (1999) and McNab (2012), but may also be at least partially influenced by the dietary patterns.

If Klasing (1999) suggested that morphological convergence could occur in birds due to similar nutritional and ecological selection pressures, we add that such convergence may also take place at the metabolic dimension.

3.4.2.12 Climate

According to our results, bird species inhabiting temperate regions display significantly higher values of $\dot{v}$ and $[\dot{p}_M]$ than species inhabiting tropical regions but only if we compare the species at their specific average adult body temperatures. The former also exhibit significantly higher

values of $\{\dot{p}_{Am}\}$ than the latter, at the reference temperature, confirming our twelfth hypothesis (Table 3.11). These higher $\{\dot{p}_{Am}\}$ values in temperate bird species are consistent with the hypotheses focusing on the capacity to exhibit rapid energy intake. However, the higher values we also observed regarding $\dot{v}$ and $[\dot{p}_M]$ help to constraint the capacity to hold large amounts of reserve (for instance, no significant difference was found regarding the fasting capacity), and this complies with the flight requirements of migration. Supporting the role of migration in explaining the differences we observed in metabolism is the fact that Climate and Migration are significantly, yet moderately correlated ($r(37) = 0.57$, $p = 1.12 \times 10^{-4}$). The other factor that is also significantly and moderately correlated with Climate is Foraging habitat ($r(37) = 0.42$, $p = 6.94 \times 10^{-3}$).

3.4.2.13 Conservation status

The only significant difference regarding the estimated DEB parameters' values and the conservation status of our sampled species is related to the amount of energy invested in maturation up to the moment of fledging. The five species classified as being Endangered or Vulnerable have significantly higher values of E_H^x than the species classified with the Least Concern statute. However, the difference is also visible regarding E_H^b despite not being significant. Higher energy requirements up to fledging may contribute negatively to any situation of threat that a species may be facing, such as habitat degradation, increased difficulty to find food or any of the many other known constraints. However, Conservation status as a factor is also significantly, yet moderately correlated with Flight ($r(37) = 0.43$, $p = 5.48 \times 10^{-3}$) as most of the threatened species are flightless.

The association between specific life history patterns and higher levels of threat is a possibility but further research with larger samples for each conservation status will be required.

3.4.3 Trade-offs

Taking our results into account it is possible to observe how the DEB theory allows us to estimate and anticipate metabolic differences among species exhibiting very similar phenotypes or metabolic similarities among species with different phenotypes. The trade-offs that emerge from metabolic constraints explain the differences we observe in life history traits. The next examples illustrate these facts.

The trade-off between the specific allocation to reproduction per maximum structural volume ($\dot{p}_R^m$ / L_m^3, J d^{-1} cm^{-3}) and the initial egg mass (M_E^0, C-mol), two DEB properties that we have shown to be easily estimated through the application of the standard DEB model, allows for the reproduction rate – one of the most discussed life history traits – to emerge as a metabolically constrained result (Figure 3.29). In our sample of bird species, the Great Tit (*Parus major*) is the species with the highest average maximum reproduction rate (about 16 eggs per year distributed in two clutches). The small size of the bird and low M_E^0, values but relatively high $\dot{p}_R^m$ / L_m^3 allows for such a high reproduction rate. The North Island Brown Kiwi (*Apteryx mantelli*) allocates relatively more energy to reproduction ($\dot{p}_R^m$ / L_m^3 = 1.55 > 1.27 J d^{-1} cm^{-3}) but the significantly larger eggs (M_E^0 = 5.89 > 2.24 × 10^{-2} C-mol) constrain the reproduction rate to about 6 eggs per year, distributed in two clutches.

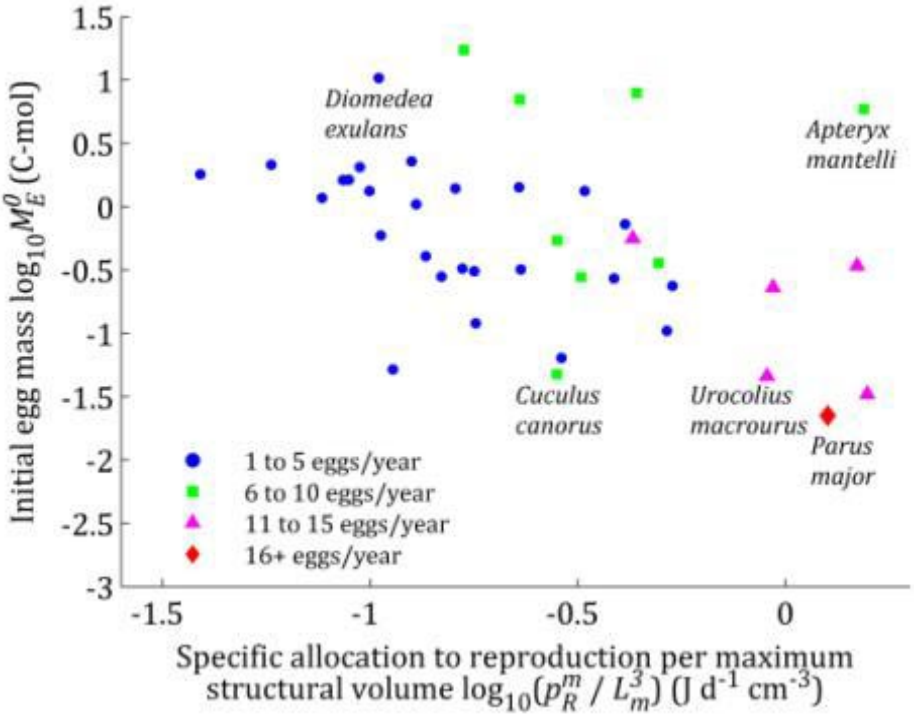

Figure 3.29 – Initial egg mass (M_E^0, C-mol) as a function of the specific allocation to reproduction per maximum structural volume ($\dot{p}_R^m$ / L_m^3, J d^{-1} cm^{-3}) at the reference temperature of 293 K. Each marker type corresponds to a specific range of reproduction rates (average number of eggs per year). A few data points corresponding to particular species discussed in the text are labelled.

We can illustrate the effect of distinct investments in reproduction and maturation quite easily by comparing two species with very different life histories: the North Island Brown Kiwi and

the semi-altricial Wandering Albatross (*Diomedea exulans*). Both species lay big eggs of similar wet weight (443 g ≈ 484 g) and have long incubation periods (83 d ≈ 80 d). However, the Albatross allocates a larger fraction of energy to somatic growth than the Kiwi (κ = 0.998 > 0.791) but a much lower fraction to maturity maintenance ($\dot{p}_J^p / L_m^3$ = 9.27 × 10^{-5} < 0.62 J d^{-1} cm^{-3}) and reproduction ($\dot{p}_R^m / L_m^3$ = 0.1 < 1.55 J d^{-1} cm^{-3}). As a result, despite the fact that the Kiwi hatchlings are lighter than the Albatross hatchlings (239 g < 379 g), the reproduction rate of the Albatross is much lower (one hatchling every other year). The amount of energy invested in maturity during the incubation period by the Kiwi is much higher than the amount invested by the Albatross (5.77 × 10^2 kJ > 4.84 kJ). As a consequence the precocial Kiwi exhibits a higher value of μ_H^b than the semi-altricial Albatross (1.95 × 10^2 kJ mol^{-1} > 1.5 kJ mol^{-1}). The trade-off lies on the growth rate with the Albatross nestling exhibiting a von Bertalanffy growth rate that is much higher than that of the Kiwi, at the same reference temperature (7.61 × 10^{-4} d^{-1} > 2.29 × 10^{-4} d^{-1}) or at each specific average body temperature (1.88 × 10^{-2} d^{-1} > 4.5 × 10^{-3} d^{-1}, respectively). A life history such as that of the Wandering Albatross, where the allocation to growth and to locomotion costs (i.e., somatic maintenance costs) are considerable (Teixeira et al., 2014) clearly demands a trade-off with reproduction.

Two bird species sharing similar phenotypes may also exhibit distinct life history traits such as different reproduction rates. The altricial Blue-naped Mousebird and the altricial Common Cuckoo share a similar egg wet weight (3 g and 3.22 g, respectively) and incubation period (approximately 12 d) but both species allocate a large fraction of energy to somatic growth (κ = 0.991 and κ = 0.998, respectively). The Mousebird hatchling weighs slightly less than the Cuckoo (W_w^h = 2.34 g and W_w^h = 2.6 g, respectively) and exhibits a lower von Bertalanffy growth rate at the reference temperature ($\dot{r}_B$ = 2.82 × 10^{-3} d^{-1} and $\dot{r}_B$ = 3.92 × 10^{-3} d^{-1}, respectively) or at body temperatures ($\dot{r}^T{}_B$ = 7.29 × 10^{-2} d^{-1} and $\dot{r}^T{}_B$ = 10.34 × 10^{-3} d^{-1}, respectively). Despite the smaller mass, the Mousebird hatchling has had a larger amount of energy invested in maturation during the embryonic stage than the Cuckoo (E_H^b = 199.33 J and E_H^b = 46.5 J, respectively). In about 3 months, the Mousebird has approached the average adult body weight (W_w^h = 56 g) but in that same time period the Cuckoo has approached an average adult body weight two times larger (W_w^h = 115 g). Despite the phenotypically similar incubation life histories, the metabolic differences between the Mousebird and the Cuckoo allow distinct adult life histories. Both species approach their average adult body weight in similar time periods and start to reproduce during the first breeding season, approximately one year after they hatched. The smaller average adult body weight of the Mousebird may have its disadvantages (e.g., higher predation risks) but coupled with a slightly larger allocation of energy to maturity and reproduction, it achieved an annual average reproduction rate that is higher than the Cuckoo's (the Mousebird will produce about six clutches a year with two or three eggs per clutch and the Cuckoo will lay on average nine eggs a year, distributing them in several host species' nests).

It is clear that the major trade-off between growth, maturity and reproduction is highly determined by the primary DEB parameter with the lowest degree of variation in birds – the κ rule. The constraint represented by this extremely relevant allocation rule can be further illustrated through the pattern it establishes with the dry mass-specific maturity at birth (μ_H^b, J mol^{-1}). The metabolic possibility of investing more or less energy into maturity per unit of dry mass, and therefore establishing the level of physiological complexity in organisms seem to be highly constrained by the allocation defined by the κ rule. In birds, as we have seen, such constrain may have led to behavioural adaptations regarding parental care (Figure 3.30).

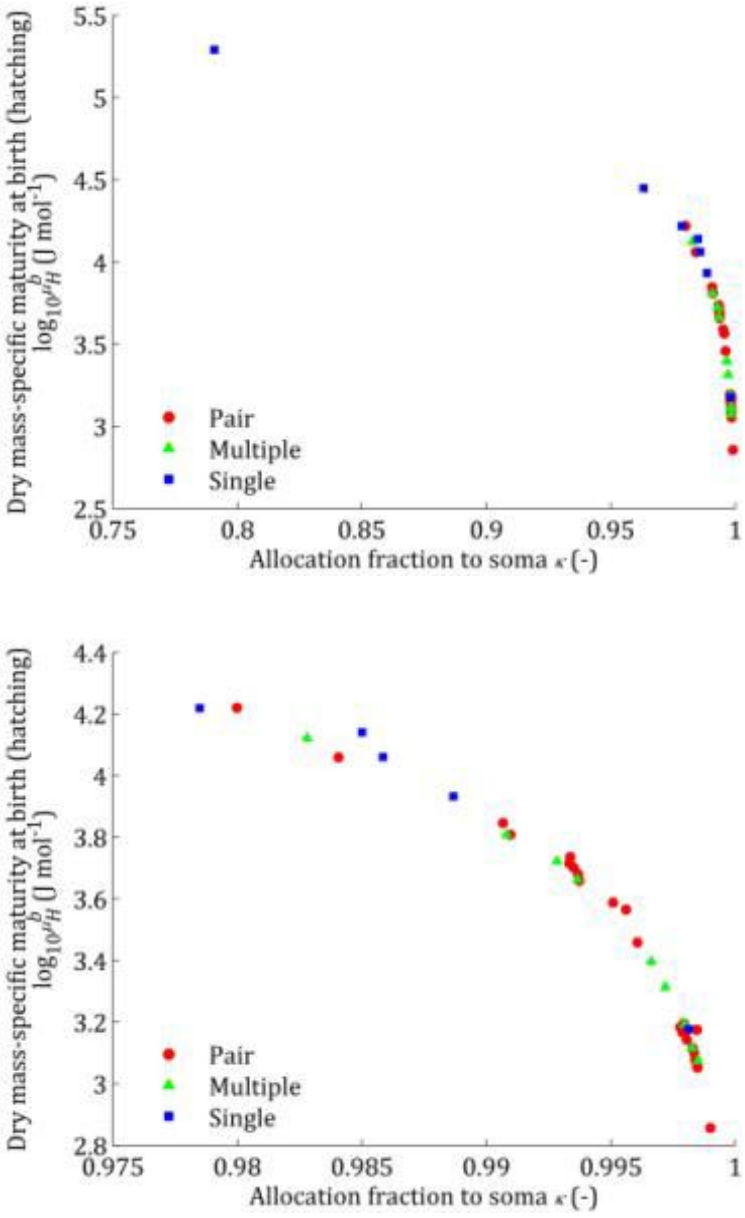

Figure 3.30 – The dry mass-specific maturity at birth (hatching) (μ_H^b, J mol^{-1}) as a function of the allocation fraction to soma (κ, -) at the reference temperature of 293 K. The plot on the right excludes the two highest values regarding the North Island Brown Kiwi (*Apteryx mantelli*) and the Red Junglefowl (*Gallus gallus*). The markers refer to the kind of parental care provided to the hatchling exhibited by each species: square – single progenitor; circle – pair of progenitors, triangle – multiple helpers.

3.5 Conclusions

The application of DEB theory provides valuable insights to the study of the evolution of the life history of birds and allows for a mechanistic and metabolically explicit approach to life history theory. Through the research on how different ecological and behavioural strategies are associated with the diversity of values estimated for most DEB parameters, functions and properties, relevant insights on how metabolic processes may have constrained the life history traits exhibited by bird species. Many researchers have highlighted the need to identify and describe the internal, proximate mechanisms that link metabolism to life history. We have shown that DEB parameters and functions may actually correspond to these proximate mechanisms and may constitute endogenous drivers of variation.

Our study has provided evidence of the extremely important role that body size has in determining the distribution of many metabolic properties of birds, even in cases when this is not expected (based in physics and not in ecological or evolutionary adaptations) such as with the specific allocation to reproduction per maximum structural volume of the species. It has also provided evidence of the way certain ecological factors are important to understand specific metabolic properties. For instance, despite the important relationship between body size and the surface-specific assimilation rate, the distribution of values regarding this parameter was significantly and highly associated with migratory habits. We have shown how any deviation from what is physically expected has evolutionary meaning.

By analysing several ecological factors we have demonstrated how the apparent co-evolution of several DEB parameters and properties in birds is consistent with the waste-to-hurry hypothesis, which may have been throughout the evolution of modern bird species, with somatic maintenance costs increasing as a response to increased production and growth rates and ultimately determining the evolution of altriciality from earlier, precocial ancestors. Further studies will certainly enrich the current knowledge regarding this strategy.

Several other hypotheses suggested by authors in previous studies have been confirmed and a broad perspective on how the co-evolution of those metabolic processes represented by the DEB parameters and several ecological and behavioural strategies may have played out throughout the evolution of modern birds. We have demonstrated how clear is the current classification of the Neornithes in two different Superorders and how important the development type, within the altricial-to-precocial spectrum, and the emergence of flight and migratory capacities seem to have been in the evolution of modern birds.

A progressive decline in body size or a miniaturization trend such as Lee *et al.* (2014) suggested across the evolution of the Neognathae may have co-evolved with the emergence of flight and the ability to colonize arboreal habitats (Benton, 2014). Flight has allowed for new arboreal habitats to be explored, simultaneously demanding higher locomotion costs and enabling diets with richer caloric content. Lower reserve mobilisation rates, constraining the reserve and fasting capacities and lowering the total weight to carry in flight, may have facilitated the evolution of this capacity. The differences we observed regarding the mating system, nest use and parental care also support this perspective with monogamy, more complex nests and increased parental care emerging from the increased demands of the altricial hatchlings and the occupation of complex three-dimensional habitats such as tree canopies, as Dyke & Kaiser (2010) suggested. A transition from diets mostly dependent on vegetal materials to those constituted by other animals, offering richer caloric content and requiring shorter and lighter digestive tracts may have co-evolved with this scenario. Finally

we demonstrated how the DEB theory allows us to understand how the apparent trade-offs between life history traits such as the reproduction rate and egg size actually emerge from specific metabolic constraints. Through the study of these trade-offs we may anticipate with higher accuracy how the currently living bird species will adapt to the global changes that are in course and ultimately design more effective conservation strategies.

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4 A new perspective on the growth pattern of the Wandering Albatross (*Diomedea exulans*) through DEB theory

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Abstract

The Wandering Albatross (*Diomedea exulans*) and other seabirds exhibit a growing pattern that includes a period of body mass decrease before fledging. Several hypotheses have been suggested to explain it without success. We hypothesized that: 1) chicks and adults have similar metabolic traits regulating assimilation, growth and maturation; 2) there is a difference in locomotion effort between chicks and adults, and 3) chicks are exposed to a decline in food availability before fledging. This set of hypotheses allows for an energy surplus to be available and stored in reserve during the first months of development, explaining the mass recession that starts before fledging and the fact that adults keep a lower weight than fledglings, throughout the rest of their life span. To test this set of hypotheses we applied the Dynamic Energy Budget (DEB) theory. Using a small set of life-history traits and growth curves we parameterized the DEB standard model. We confirmed this set of hypotheses and estimated the pattern of decline in food availability that explains mass recession. An assessment of the daily energy intake was also performed. The implications related to that energy flux and diet composition are discussed based on current knowledge. The DEB model for the Wandering Albatross also provided estimates for the adult daily food ingested by adults (464.06 kJ kg^{-1} d^{-1}), fasting capacity (25 d), Field Metabolic Rate (4.29 W kg^{-1}) and Resting Metabolic Rate (2.87 W kg^{-1}). These values are consistent with the averages obtained in the field, suggesting that DEB may be useful to provide good estimations on a broader scale.

Keywords

Dynamic Energy Budget; Wandering Albatross; *Diomedea exulans*; growth pattern; altricial birds; metabolic rates

4.1 Introduction

4.1.1 Initial remarks

The ontogeny of birds is diverse in its characteristics and patterns. We can find this diversity in the behavioural development of chicks (Düttmann et al., 1998) or the shape of the growth curve (Knížetová et al., 1995; Mignon-Grasteau and Beaumont, 2000; Ricklefs, 1979a, 1973, 1968), among other subjects. This diversity may be the result of selective pressures that influenced the evolution of terrestrial vertebrates in general (Case, 1978) and of early birds in particular (Chinsamy and Elzanowski, 2001) giving origin to adaptation strategies (Lack, 1968; Ricklefs, 1979b) and internal constraints that we can still observe today (Ricklefs et al., 1998), particularly within the altricial-precocial spectrum (Starck and Ricklefs, 1998b). Many factors may have driven these pressures, such as competition among siblings for limited food resources (Royle et al., 1999), nest predation (Bosque and Bosque, 1995) or even embryonic determinants (Blom and Lilja, 2005). In this context, and as previous studies have highlighted, it becomes clear that ontogeny is of key importance not just for survival itself but also to reproduction later in life and therefore to population dynamics (Lindström, 1999; Sibly et al., 2012).

Regarding growth, birds generally exhibit patterns similar to those of other vertebrates. However, some differences exist, including the variation in growth rate related to changing body temperatures during the transition to endothermy (Bucher, 1983; Kooijman, 2010a; Visser, 1998) and the decrease in water content observed during ontogeny (Ricklefs, 1975). Some species of birds share the particularity of exhibiting a consistent pattern of body mass decrease before fledging. These species belong to groups such as the Falconiformes, Apodiformes or Suliformes (Phillips and Hamer, 1999) and several of them are Procellariiformes (Huin and Prince, 2000; Warham, 1990; Weimerskirch and Lys, 2000).

In Procellariiform seabirds (albatrosses, shearwaters, petrels, storm petrels, and diving petrels) body mass variation during growth has been mostly attributed to the accumulation of reserves (Phillips and Hamer, 1999), probably in the form of adipose triglycerides (Groscolas et al., 1991) and subsequent use. Some of the extreme life-history traits observed in these birds may have emerged from the constraints of the marine environment (Lack, 1968; Ricklefs, 1990; Weimerskirch and Lys, 2000) and several hypotheses have been proposed in order to explain the evolution of nestling obesity in seabirds that can be included in four main groups: a) energy storage in reserves at an early stage works as an 'energy-sink' providing extra energy for later (Obst and Nagy, 1993; Reid et al., 2000; Ricklefs, 1979b); b) stored energy provides a kind of insurance against one or several elements of stochasticity (Lack, 1968; Ricklefs and Schew, 1994; Ricklefs, 1990); c) stored energy allows for a quicker development before fledging so that adults may migrate sooner (Brooke, 1990), and d) stored energy enables a safer transition to the post-fledging period when foraging skills are still to be learned (Perrins et al., 1973; Phillips and Hamer, 1999).

The first group assumes fat accumulation to be taking place mostly during the first months of development. The evolutionary driver could be the pressure to store fat early when energetic costs are still low, for the period just before fledging. By then, energetic costs are higher, the quantity and quality of food provided by the parents may be declining but the growth quality of flying feathers still needs to be assured.

The second group considers the usefulness of fat deposits throughout the growing period. The evolutionary driver could be the stochasticity resulting from uncertain environmental conditions faced by progenitors when foraging at sea or from erratic and independent feeding strategies performed by individual parents.

The last two groups assume fat accumulation to occur mostly during the period just before fledging or the importance to have at least some of the fat previously accumulated still available when fledging and the evolutionary drivers could be mostly behavioural. Most of these hypotheses are based on external drivers but some authors have pointed out that these growth patterns may in fact emerge from physiological processes and constraints (Phillips and Hamer, 2000).

4.1.2 The Wandering Albatross

The Wandering Albatross (*Diomedea exulans*) is a sexually dimorphic Procellariiform with the longest postnatal growth found in birds (280-290 days to develop from hatchling to fledgling and 6-15 years until they breed for the first time) (Lequette and Weimerskirch, 1990; van den Hoff and Candy, 2010). Adults arrive at their breeding sites in November and every other year each pair lays a single egg in an elevated mud-nest during December and January. Incubation takes about 80 days (hatching typically occurs around mid-March) and the semi-altricial hatchlings are then brooded alternately by both adults for 21-43 days (Tickell, 1968; van den Hoff and Candy, 2010). After brooding, the chick remains alone in or near the nest, receiving intermittent feeds from either parent that visit the nest for brief periods lasting 6-12 hours to feed the chick and then return to the sea where they progressively invest in longer foraging journeys throughout the rest of the year (Arnould et al., 1996; Tickell, 1968; Weimerskirch and Lys, 2000). During the winter period chicks are therefore not only exposed to extreme weather conditions but also to high variability in parental care. In fact, several studies observed a progressive decline in the average total quantity of food brought to the chick throughout the growing season (Berrow et al., 2000; Lequette and Weimerskirch, 1990; Mabille et al., 2004; Weimerskirch and Lys, 2000; Weimerskirch et al., 2000a). The chick reaches fledging mass around November or December and leaves the nest (Tickell, 1968).

The body mass increase of Wandering Albatrosses follows a typical pattern with the most rapid increase occurring from April to July before stabilization of body mass at the end of August, when body mass peaks and chicks are about 1.5 times heavier than adults. After this, body mass decreases with chicks losing about half of their difference in wet weight from adults, before fledging occurs (Lequette and Weimerskirch, 1990; Mabille et al., 2004). The fledgling still weighs more than the adult. Structurally, the chicks grow without measurable decreases occurring. For instance, the culmen grows steadily and converges to average adult length values about 1.5 months before fledging (Lequette and Weimerskirch, 1990; Mabille et al., 2004; Weimerskirch et al., 2000a) and never decreases. Wing length grows in a similar way but accelerating as fledging approaches and at that moment wing length may actually be higher than in adults. However, the difference disappears with moulting and the decrease is probably not structural (Weimerskirch et al., 2000a).

The mean total body water (TBW) value is about 49% in adult Wandering Albatrosses, both before (49.45%) (Shaffer et al., 2001a) and after foraging trips (48.9%) (Shaffer et al., 2001b). Mabille et al. (2004) measured a similar value in chicks of about 40 days of age since hatching (50%) but also measured a decline occurring throughout the following months with TBW reaching a value of 44% in chicks of about 220 days of age.

Adult Wandering Albatrosses ingest an average of 2.1 kg of food per day when foraging for their own nutritional needs (during incubation) (Weimerskirch et al., 1994). The amount of food fed to chicks throughout the growing period declines toward the end of the austral winter mostly due to a decrease in the frequency of visits performed by each progenitor as they progressively invest in longer trips that may take as long as several weeks (Xavier et al., 2004). The diet consists mostly of pelagic cephalopod species, particularly squids from Families such as Histioteuthidae (in warmer waters) and Onychoteuthidae (in southern, colder waters) (Ceia et al., 2012; Imber, 1992; Weimerskirch et al., 2005), as well as of fish, particularly from Families such as Nototheniidae and Channichthyidae (Croxall et al., 1988). However, the relative composition of the diet seems to differ depending on the oceanic region, average foraging distance from the shore and on the foraging driver (self-feeding or chick feeding) (Adams et al., 1986; Arnould et al., 1996; Ceia et al., 2012; Weimerskirch et al., 2005; Xavier et al., 2004).

Previous studies on the daily energy expenditure of the Wandering Albatross provided estimates as low as 1.7 W kg^{-1} (Weimerskirch et al., 2002) or as high as 4 W kg^{-1} (Shaffer et al., 2001a) for the Resting Metabolic Rate (RMR) and estimates of up to 5.3 W kg^{-1} (Shaffer et al., 2001a) for the Field Metabolic Rate (FMR), using a variety of techniques (Adams et al., 1986; Arnould et al., 1996; Shaffer et al., 2001a; Weimerskirch et al., 2000b). Adult Wandering Albatrosses spend most of their time flying (Weimerskirch et al., 2007), regardless of maturity, and it has been estimated that a long lived individual may cover 8.5 Gm in a lifetime (Weimerskirch et al., 2014). Their most costly daily activities consist of lifting off from and landing on the water (Weimerskirch et al., 2000b).

4.1.3 Modelling the development of the Wandering Albatross

Three equations belonging to the Richards family of sigmoid curves have been widely used to model growth, namely the von Bertalanffy equation, the Gompertz equation and the logistic equation (Huin and Prince, 2000; van den Hoff and Candy, 2010; Weimerskirch et al., 2000a). Despite the fact that these curves have been used to model the growth pattern of many bird species with asymptotic body mass gain, the challenges of using them to model the mass growth of Wandering Albatross chicks, are clear. Therefore, specific models aiming at estimating a maximum mass assuming the absence of an asymptote were considered as necessary. A previous study fitted growth curves to the body mass data of individual chicks using a weighted least squares (WLS) technique and the proportions of chicks following each type of growth curve were Gompertz (47.1%), von Bertalanffy (40.2%) and logistic (12.6%) (Weimerskirch et al., 2000a). Recently a reverse Gompertz growth model extended with a non-linear mixed model and cubic smoothing splines within a linear mixed model has been applied (van den Hoff and Candy, 2010). Previously, the Gompertz curve had already been used in Wandering Albatrosses, coupled with a third degree polynomial equation (Weimerskirch et al., 2000a). Huin and Prince (2000) developed an equation integrating two Gompertz curves (a positive and a negative) in order to fit both the mass increase and decrease stages but this equation required five coefficients (growth rate, peak mass, age at which it was attained, loss rate and a curve shape index value) and the authors highlighted the facts that some of the parameters may be highly intercorrelated and that their confidence limits are hard to assess.

In order to test hypotheses regarding body mass recession observed in Wandering Albatrosses, and how these may be in accordance with current knowledge on the energetics of the species, it is necessary to go beyond curve fitting and actually apply a biologically explicit theory, such as the Dynamic Energy Budget (DEB) theory. This theory unifies the common characteristics and constraints found in the energetics of organisms providing a framework to model the

uptake and use of energy and nutrients throughout the life cycle of a species (Kooijman, 2010a; Sousa et al., 2010, 2008).

This paper is organized as follows: in section 2 we a) present our hypothesis to explain the growth pattern of this species; b) synthesize the collected data on the metabolism and development of the Wandering Albatross, and c) compute the Wandering Albatross DEB parameters; in section 3 we present our results and in section 4 we discuss these results considering current knowledge on the diet, energy expenditure and foraging behaviour of the Wandering Albatross.

4.2 Methodology

4.2.1 Hypothesis on the growth pattern

When considering the hypotheses explaining the pattern of body mass variation, some observations on the biology of Wandering Albatrosses were regarded to be key: a) fledglings weigh more than adults when they leave the nest (Groscolas et al., 1991; Lequette and Weimerskirch, 1990; Mabille et al., 2004); b) body mass decrease takes place during the last two and a half months and continues after fledging until the average adult mass is attained (Weimerskirch et al., 2014); c) food provisioning declines during the last months before fledging (Weimerskirch and Lys, 2000); d) TBW also declines during those last months (Mabille et al., 2004); e) wing length is growing throughout the whole period with some of the most important primary feathers for flying reaching a viable length just prior to fledging (Berrow et al., 1999); f) structural adult length is reached before fledging (Lequette and Weimerskirch, 1990; Mabille et al., 2004) and g) locomotion is responsible for a considerably higher fraction of the daily energy expenditure after fledging (Weimerskirch et al., 2002, 2000b).

Taking all of the above into consideration, we formulated the hypothesis that the difference between the adult daily energy expenditure and the chick daily energy expenditure, due to considerably different locomotion costs (relative to each body size), may help to explain the observed growth pattern. Metabolically, chicks and adults of the same species share the same main characteristics. This means that regarding most processes (e.g. specific assimilation rates), no significant differences should be observed between the two. In circumstances where food is available and generously provided, the absence of expensive locomotion activities such as frequent lifting off and landing on water, could be enough to explain a growth rate that aims at a higher body mass value than that of the adult. The general decline in food provisioning and TBW may drive the decrease in body mass, and the immediate increase in locomotion costs after fledging may explain how the average adult body mass is maintained.

Based on this hypothesis we followed an approach (Figure 4.1), detailed in the next sections, through which we: a) assembled a data set with several of the main life history traits of the Wandering Albatross, including average values for single data-point characteristics (henceforth designated as “zerovariate data”); b) used the data to compute the values of the standard DEB parameters that would accurately describe those traits; c) used data on the locomotion costs to estimate the lower somatic maintenance costs of the chicks; d) ran the DEB model to test the difference in costs and estimate the variation in energy intake from food, while fitting expectations to body mass and length growth curves, and e) estimated how fasting capacity changes and validated our model assessing the FMR and RMR for the species.

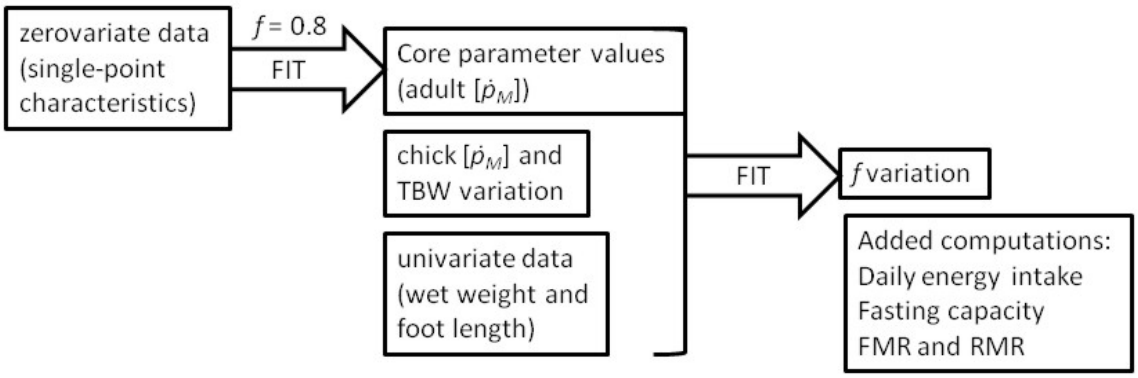

Figure 4.1 – Methodological approach. Our methodological approach was processed in three stages: a) estimation of DEB parameter values using zerovariate data, b) estimation of different somatic maintenance costs for the chick due to lower locomotion costs and inclusion of a total body water (TBW) variation function, and c) new estimation of DEB parameter values using zerovariate and univariate data, estimation of the expected variation in the scaled functional response (f) and additional computations. FMR refers to the field metabolic rate and RMR to the resting metabolic rate.

4.2.2 Data used

Average values observed for several life-history traits of the Wandering Albatross were collected from the literature (Table 4.1). All the values considered were taken from combined sexes samples. Despite the fact that Wandering Albatross chicks are sexually dimorphic and despite typically higher rates for males than females (due to higher amounts of food delivered to male chicks) the period of mass increase to the asymptote and the period of mass decline are similar for chicks of both sexes (with similar proportionate rates of mass loss) and therefore considering an average and unbiased sex ratio, average mass values can be taken to represent the chick population (van den Hoff and Candy, 2010).

Sexual maturity (age at puberty) corresponds to the earliest records of age at first breeding observed to have taken place in this species (6 years). On average individuals start to breed only around 10 years of age (Tickell, 1968) but physiological maturity is probably achieved much earlier than that and the delay between maturity and the onset of reproduction is probably due to behavioural factors. Maximum reproduction was considered to take place at the typical rate (1 egg every two years) and maximum life span corresponds to the highest age ever recorded for an animal of this species (60 years).

The average hatchling body mass and the age at fledging collected from the same study from which body mass and culmen length growth measurements were taken. Average body temperature was available in the literature but the average incubation temperature had to be based on studies on the Laysan (*Phoebastria immutabilis*) and Black-Footed Albatrosses (*Phoebastria nigripes*).

The univariate data considered were culmen length, body mass, and absolute TBW measurements obtained throughout the chick growing period from the colonies in the Île de la Possession (Crozet Archipelago) in 1985 (Lequette and Weimerskirch, 1990) and 2000 (Mabille et al., 2004) (Table 4.2). Previously, differences in growth rates between the populations of distinct archipelagos have been measured but fledging typically occurs with similar values and the differences in growth rates may be due to historical differences in productivity of foraging areas (van den Hoff and Candy, 2010). Lequette and Weimerskirch

(1990) took measurements from chicks reared by pairs with different levels of experience. We only considered values obtained from chicks reared by pairs with extensive experience. This study had a larger sample (n = 31) than that of Mabille et al. (2004) (n = 10) which also had a lower set of sampling sessions. Based on this, we chose to use the measurements from the first study. Culmen length was selected as the best available physical element to be modelled in terms of structural length, considering the absence of total body length measurements spanning the whole growing period.

The absolute TBW values were only available in the study of Mabille et al. (2004).

Table 4.1 – Wandering Albatross life history traits used as zerovariate data to estimate the DEB standard model core parameters ([1] Tickell, 1968; [2] Lequette and Weimerskirch, 1990; [3] Cramp and Simmons, 1977; [4] Rahn, 1991; [5] Warham, 1971).

Trait	Abbreviation	Observed	Reference
Age at hatching (d)	a_h	79.5	[1]
Age at fledging (d)	a_x	264	[2]
Age at puberty (d)	a_p	2190	[1]
Maximum life span (d)	a_m	21900	[1]
Adult (ultimate) culmen length (cm)	CL_∞	16.46	[2]
Hatchling wet weight (g)	W_w^h	379	[2]
Adult wet weight (g)	W_w^∞	7858.5	[3]
Maximum reproduction rate (#/d)	$\dot{R}_\infty$	1.37×10^{-3}	[1]
Egg temperature (K)	T_{ah}	308.8	[4]
Adult body temperature (K)	T_{am}	312.6	[5]

Table 4.2 – Univariate data collected throughout the Wandering Albatross chick growing period in Île de la Possession (Crozet archipelago) (sexes combined). TBW corresponds to the Total Body Water.

	(Lequette and Weimerskirch, 1990) (n = 31)		(Mabille et al., 2004) (n = 10)	
Age (d)	Body mass (kg)	Culmen length (cm)	Absolute TBW (L)	Wet weight/ Dry weight
10	1.07	5.09	-	-
25	2.58	6.70	-	-
40	3.89	8.01	2.12	2.02
55	5.33	9.26	-	-
70	6.45	10.49	3.74	1.98
85	7.82	11.49	-	-
100	8.83	12.62	5.06	1.99
115	9.68	13.52	-	-
130	10.77	14.38	5.42	1.89
145	11.28	15.05	-	-
160	11.87	15.59	5.85	1.88
175	11.72	16.02	-	-
190	12.38	16.26	5.89	1.84
205	11.91	16.42	-	-
220	12.16	16.44	5.57	1.77
235	11.43	16.46	-	-
250	10.93	16.46	-	-
264	10.05	5.09	-	-

4.2.3 DEB parameters

The standard DEB model describes the ontogeny of an organism through the dynamics of three state variables – structure ($V = L^3$), reserve (E) and maturity (E_H) – and uses a set of core parameters complemented by auxiliary parameters and compound parameters.

In order to estimate the values for the core parameters (Table 4.3) (Lika et al., 2011a) we used the software DEBtool (MATLAB version 7.3.0) (Kooijman, 2010b). For the purpose of running DEBtool's routines, two files were programmed in MATLAB (THE MATHWORKS INC., 2012), using as input the zero and univariate data as well as assumed parameter values to start the estimation procedure. The estimation procedure follows the "covariation method" (Lika et al., 2011a). With this method, parameter estimates are based on the simultaneous minimization of a weighted sum of squared deviations or of the negative log likelihood function between the data we inserted and the estimated values, both in a single-step procedure. Similarly to previous studies (Huin and Prince, 2000; Weimerskirch et al., 2000a) we chose a WLS criterion to fit the estimates to the set of zero and univariate data.

We used some auxiliary parameters to convert volume, mass, energy and physical measurements or to correct rates according to the specific body temperature (Table 4.4). Detailed descriptions are available in Lika et al. (2011).

Some of the parameters were assumed to have a predetermined value. The reference temperature (T_{ref}) of 293 K and Arrhenius temperature (T_A) of 1.5×10^4 were chosen in order to maintain comparability with other species' parameter sets available in the "Add_my_pet" library (Kooijman, 2014a). The same logic justified the choice of 0.01 for the Gompertz stress coefficient (S_G). Food availability was included as a variable through the "scaled functional response" (f), a dimensionless variable based on the Michaelis-Menten function ($f = X / (K + X)$), also considered as a Holling type II functional response, where X represents food and K the half-saturation coefficient or Michaelis-Menten constant. At any moment f can assume a value from 0 (no food) to 1 (*ad libitum*). Values above 1 correspond to overfeeding. For the purpose of estimating the core parameter values, food was assumed to be relatively available ($f = 0.8$) and stable. In this manner, the growth rate we obtain corresponds to the von Bertalanffy type. The digestion efficiency (κ_X) was considered to be 0.8 based on a nitrogen-corrected cephalopod energy assimilation efficiency of 81.82% estimated for Wandering Albatrosses (Battam et al., 2010) and utilization efficiencies of 81.3% and 76.1% for squid and fish diets respectively, measured in King Penguins (*Aptenodytes patagonicus*) (Adams, 1984; Cooper, 1978). The reproductive efficiency (κ_R) value was chosen by default to be 0.95 in the absence of more detailed information. The surface-specific somatic maintenance ($\{\dot{p}_T\}$) was considered to be zero on the assumption that we are modelling growth within the thermal-neutral zone for this species. The specific densities of structure and reserve (d_V and d_E) were considered to be identical and their value (0.5) was based on TBW values (wet weight / dry weight ratio of 2). The chemical potentials considered for structure (μ_V) and reserve (μ_E) were the default values of 500 and 550 kJ mol^{-1}, respectively. The chemical indices for structure (n_V) and reserve (n_E) were considered to be identical and corresponded to 1 atom of carbon, 1.8 atoms of hydrogen, 0.5 atoms of oxygen and 0.15 atoms of nitrogen, per atom of carbon respectively. These are approximate default values for dry mass (Lika et al., 2011a) used in the absence of more detailed information on the chemical composition of albatrosses. The molecular weights of structure (w_V) and reserve (w_E) are obtained from these indices and also equal (23.9 g mol^{-1}).

By applying the covariation method we obtained the values of the standard DEB model core parameters that provide the better estimates for all the life-history traits considered while simultaneously allowing for a good fit to the observed culmen length growth curve.

Some compound parameters were estimated using the core parameters, namely the maximum specific assimilation rate ($\{\dot{p}_{Am}\} = z\,[\dot{p}_M] / \kappa$) (J d^{-1} cm^{-2}), the energy investment ratio ($g = [E_G]\,\dot{v} / \kappa\,\{\dot{p}_{Am}\}$) and the maximum length ($L_m = [E_G]\,\dot{v} / [\dot{p}_M]\,g$) (cm).

For the growth curve fitting procedure, the parameters $\dot{v}$, $\{\dot{p}_{Am}\}$ and $\dot{k}_J$ were corrected from the reference temperature (293 K) to the Wandering Albatross body temperature (312.6 K), resulting in values of 3.24 cm d^{-1}, 1.85×10^4 J d^{-1} cm^{-2} and 3.15×10^{-4} d^{-1} respectively.

Table 4.3 – The core parameters of the standard DEB model and their respective summarized descriptions. More details are available in Lika et al. (2011).

Parameter	Abbreviation	Summarized description
Zoom factor (-)	z	Controls the maximum length via the specific assimilation.
Maximum surface-area-specific searching rate ($dm^3\,d^{-1}\,cm^{-2}$)	$\{\dot{F}_m\}$	Controls food intake if food is not abundant and has no effect at abundant food.
Digestion efficiency (-)	κ_X	Specifies the fraction of energy in food that is fixed in reserve.
Defecation efficiency (-)	κ_X^P	Specifies the fraction of energy in food that ends up as faeces.
Energy conductance ($cm\,d^{-1}$)	$\dot{v}$	Controls the reserve mobilisation.
Allocation fraction to soma (-)	κ	Controls the allocation of mobilised reserve to somatic maintenance and growth as opposed to maturity maintenance and maturation of reproduction.
Reproduction efficiency (-)	κ_R	Fraction of reserve allocated to reproduction that is fixed in the reserve of offspring.
Volume-specific somatic maintenance (J $d^{-1}\,cm^{-3}$)	$[\dot{p}_M]$	Controls the sink of reserve linked to structural volume, mostly due to turnover of structure, behaviour and transport.
Surface-specific somatic maintenance (J $d^{-1}\,cm^{-2}$)	$\{\dot{p}_T\}$	Controls the sink of reserve linked to structural surface area.
Maturity maintenance rate coefficient (d^{-1})	$\dot{k}_J$	Controls the sink of reserve linked to maturity.
Specific cost for structure (J cm^{-3})	$[E_G]$	Reserve energy required to synthesize a unit volume of structure.
Maturity at birth (J)	E_H^b	Controls the timing of and the size at birth, i.e. the moment assimilation is switched on.
Maturity at fledging (J)	E_H^x	Controls the timing of fledging, i.e. the moment at which self-feeding starts.
Maturity at puberty (J)	E_H^p	Controls the timing of and the size at puberty, i.e. the moment at which investment into maturation is re-directed to reproduction.
Weibull ageing acceleration (d^{-2})	$\ddot{h}_a$	Controls the mean life span in a way that hardly depends on food density (because the increased respiration is cancelled by dilution by growth).
Gompertz stress coefficient (-)	S_G	Controls the mean life span, but in ways that depend on food density.

Table 4.4 – The auxiliary parameters of the standard DEB model used in this study to correct for body temperature and to convert volume, mass, energy and physical measurements (Lika et al., 2011a).

Parameter	Abbreviation	Summarized description
Reference temperature (K)	T_{ref}	Working temperature for which parameter values are given.
Arrhenius temperature (K)	T_A	Controls the effect of temperature on rates.
Shape coefficient (-)	δ_M	Converts physical to volumetric structural length.
Specific densities (g cm^{-3})	d_V, d_E	Converts volume to mass for each organic compound (V indicates structure and E reserve).
Chemical potentials (J mol^{-1})	μ_V, μ_E	Converts moles to energy.
Chemical indices (# C^{-1})	n_V, n_E	Relates the frequency of chemical elements (C, H, O and N) to C.
Molecular weights (g mol^{-1})	w_V, w_E	The molecular weight of each organic compound is obtained by multiplying the chemical indices with the atomic mass of each element (C = 12 g mol^{-1}; H = 1 g mol^{-1}; O = 16 g mol^{-1}; N = 14 g mol^{-1}).

4.2.4 DEB model

In order to compute the values of each DEB state variable (structure, reserve and maturity), at each moment of the chick's growth period, we used a function that solved the relevant ordinary differential equations (ODE's) through that time span. The equations to be solved corresponded to the scaled reserve density ($e = \dot{v}\, E \,/\, L^3 / \{\dot{p}_{Am}\}$), where E (J) is the amount of energy in the reserve, the specific growth rate ($\dot{r} = \dot{v}\,(e/L - 1/L_m) \,/\, (e + g)$) (d^{-1}) and the scaled mobilisation flux ($\dot{p}_C = E\,(\dot{v}/L - \dot{r})$) (J d^{-1}). With these we calculated the derivatives for structure, reserve and maturity:

$$\frac{dL}{dt} = \frac{\dot{r}\, L}{3} \qquad \frac{dE}{dt} = \{\dot{p}_{Am}\}\, f\, L^2 - \dot{p}_{\mathrm{C}} \qquad \frac{dE_H}{dt} = (1-\kappa)\, \dot{p}_C - \dot{k}_J\, E_H$$

The culmen physical length resulted from applying the adequate shape coefficient factor to the volumetric length (L/δ_M).

4.2.5 Somatic maintenance costs for the chick

In the DEB standard model, the energetic costs related to locomotion are included in the volume-specific somatic maintenance costs ($[\dot{p}_M]$). By calibrating a model with life-history traits that refer to the whole life cycle, the costs associated with locomotion are averaging what may be considerably different investments in locomotion performed in different stages of that cycle. Before fledging, chicks are permanently in or near the nest but after fledging they spend about 55.7% of their time flying (Weimerskirch et al., 2007), an activity in which albatrosses are very efficient but that requires the bird to be able to lift off from and land on the water 15 times a day on average (Weimerskirch et al., 2000b). The relationship between metabolic rates and the heart rate of Wandering Albatrosses has been previously studied (Weimerskirch et al., 2002, 2000b). According to these studies, the most costly activity consists of lifting off from and landing on the water (heart rate of 230 beats min^{-1}, compared to 65 beats min^{-1} when resting on land). The average heart rate measured by Weimerskirch et al. (2000b) considering a whole foraging trip (i.e. including all the activities) is 97.4 beats min^{-1}. Using these values, we estimated a heart rate of 93,600 beats d^{-1} for an adult resting on land and 140,256 beats d^{-1} for an adult during a foraging trip. The difference between the two estimated daily heart rates reflect the investment in lifting off, flying and landing – the costs we want to exclude from the volume-specific somatic maintenance costs of the chick. For that purpose we estimated the ratio between these two values (0.67) and multiplied it by the value of $[\dot{p}_M]$ (which we will henceforth designate as $[\dot{p}_M]^{FMR}$). We considered the result to be an estimate of what should be the volume-specific somatic maintenance costs of the chick. This value would correspond to that of a full-time resting adult and will therefore be designated as $[\dot{p}_M]^{RMR}$.

4.2.6 Food availability before fledging

In order to estimate the variation in energy available (in the food provided by the progenitors) throughout the growth period, a function for f was included, allowing for this parameter to adjust according to a linear function (f = a t + b). The coefficients were allowed to covariate so that the best fit to the wet weight could be obtained.

We also took into account the change in TBW measured by Mabille et al. (2004) and plotted the wet weight / dry weight ratio (*wdratio*) (Table 4.2). The ratio decline follows a linear pattern and by applying a simple regression we obtained the function whereby *wdratio* = $-1.37e^{-3}t$ + 2.09 (R^2 = 0.94).

To estimate the wet weight throughout the growing period we used the equation:

$$W_w = L^3 \, (1 + f \, \omega) \, d_V \, wdratio$$

In this equation, ω corresponds to the relative contribution of reserve to weight ($\omega = \{\dot{p}_{Am}\} \, w_E \, / \, \dot{v} \, d_V \, \mu_E$).

4.2.7 Daily food energy content and fasting capacity

After estimating the variation in *f* that fits the model to the total body mass variation observed in the chicks, we estimated the flux of energy available in the food provided to the chick throughout the growing period, $\dot{p}_X$ (J d^{-1}) using the following equation:

$$\dot{p}_X = \frac{\{\dot{p}_{Am}\} \, f \, L^2}{\kappa_X}$$

Using the same equation, we also estimated the expected energy available in the daily food ingested by adults.

Fasting capacity (t_s) corresponds to the amount of time during which the organism, once deprived of food, still has enough energy stored in reserve to cover the specific somatic maintenance costs. For the adult we considered the ratio between the specific maximum reserve capacity ($[E_m] = \{\dot{p}_{Am}\} \, / \, \dot{v}$)and $[\dot{p}_M]^{FMR}$. For the chick we used the ratio between the energy available in the reserve, per unit of structural volume ($E \, / \, L^3$) and $[\dot{p}_M]^{RMR}$, for each moment in time.

4.2.8 Metabolic rates

The FMR is generally measured in free-ranging animals through a variety of techniques that frequently provide distinct results. DEB theory offers the possibility to estimate what could be considered an expected value for a FMR, using the following equation (with the rates corrected for body temperature):

$$\text{FMR} = [\dot{p}_M]^{FMR} \, L^3 + \dot{k}_J \, E_H^p$$

We applied the same equation to estimate RMR (W) but this time using $[\dot{p}_M]^{RMR}$.

4.3 Results

The first set of results consists on the estimated values for the core parameters of the DEB standard model (Table 4.5). With this set, the goodness of fit (defined as the sum of the absolute differences between observed and expected values, divided by the observed values) achieved a value of 0.93. However, this set of parameters would not allow for body mass to exhibit a pattern of mass recession.

A $[\dot{p}_M]^{FMR}$ of 42.349 J d^{-1} cm^{-3} resulted in an estimated value of 28.374 J d^{-1} cm^{-3} for the $([\dot{p}_M]^{RMR}$, after applying the daily heart rate ratio.

A second fitting procedure allowed for a final set of parameter values (Table 4.5) to be estimated, using the previous set of parameter values as initial parameters, both $[\dot{p}_M]$ values and the TBW decline function. All the parameters were allowed to change in order for a fit to the body mass growth curve (Figure 4.2) and to the culmen length curve (Figure 4.3) to be estimated. If we compare the expected culmen growth curve that would result from the first set of parameters to the final one (Figure 4.3), we see that they are very similar, with the first curve reaching a value slightly higher (1.7%) than the final length and then decreasing towards that same final length. However, the curvature is slightly more realistic with the final set. The slight downward curvature observed for the last few days before fledging would hardly be measurable. Despite the direct relationship between structural length and physical measurements taken from parts of the body, any slight decrease in structural length would probably not be visible in the culmen, which has a bony composition. To model an actual decrease in structure in a thermodynamic consistent way would require a much more complex DEB model (Tolla et al., 2007).

By aiming at the best fit to the observed body mass variation, we obtained an equation whereby $f = -1.96 \times 10^{-3}\ t + 1.07$ (Figure 4.4). The decline in f described through this equation complements the decline in TBW and helps to explain the observed decline in body mass.

The expected energy flux from the food provided to the chick throughout the growing period, $\dot{p}_X$ (kJ d^{-1}) (Figure 4.5) starts with a value of 643.81 kJ d^{-1} just after the chick hatches, reaching 4,996.04 kJ d^{-1} around 172 days of age and decreasing down to a value of 3,861.67 kJ d^{-1} just before fledging. The expected energy available in the daily food ingested by adults is 3,646.83 kJ d^{-1} (or 464.06 kJ kg^{-1} d^{-1}).

Regarding the fasting capacity, we estimated that an adult should have an approximate fasting capacity of about 25 days. We also estimated that the chick's fasting capacity increases during brooding to a value of about 37 days and then progressively declines reaching a value similar to that of the adult (22 days) by the time when fledging occurs (Figure 4.2).

Concerning the species metabolic rates, we estimated a FMR of 33.74 W (or 4.29 W kg^{-1}) and a RMR of 22.56 W (or 2.87 W kg^{-1}).

Table 4.5 – The application of the covariation method allowed for the estimation of values for the core parameters of the DEB standard model, at the reference temperature of 293 K. The values were initially obtained using zerovariate data (1st fit) and later estimated again after estimating $[\dot{p}_M]$ for the pre-fledging period and using zerovariate data and two sets of univariate data: body mass and culmen length growth (2nd fit).

Parameter	Values	
	1st fit	2nd fit
z (-)	17.775	17.807
δ_M (-)	8.306×10^{-1}	1.074
$\dot{v}$ (cm d^{-1})	3.029×10^{-2}	2.935×10^{-2}
κ (-)	9.972×10^{-1}	9.992×10^{-1}
$[\dot{p}_M]$ (J d^{-1} cm^{-3})	42.349	40.695
$\dot{k}_J$ (d^{-1})	3.884×10^{-7}	2.749×10^{-7}
$[E_G]$ (J cm^{-3})	1.308×10^{4}	1.307×10^{4}
E_H^b (J)	1.002×10^{4}	2.36×10^{3}
E_H^x (J)	1.311×10^{6}	5.417×10^{5}
E_H^p (J)	1.454×10^{7}	1.491×10^{7}
$\ddot{h}_a$ (d^{-2})	2.409×10^{-15}	2.694×10^{-15}
f function slope	0	-1.963×10^{-3}
f function intercept	0.8	1.0
$[\dot{p}_M]$ (pre-fledging) (J d^{-1} cm^{-3})	42.349	27.214

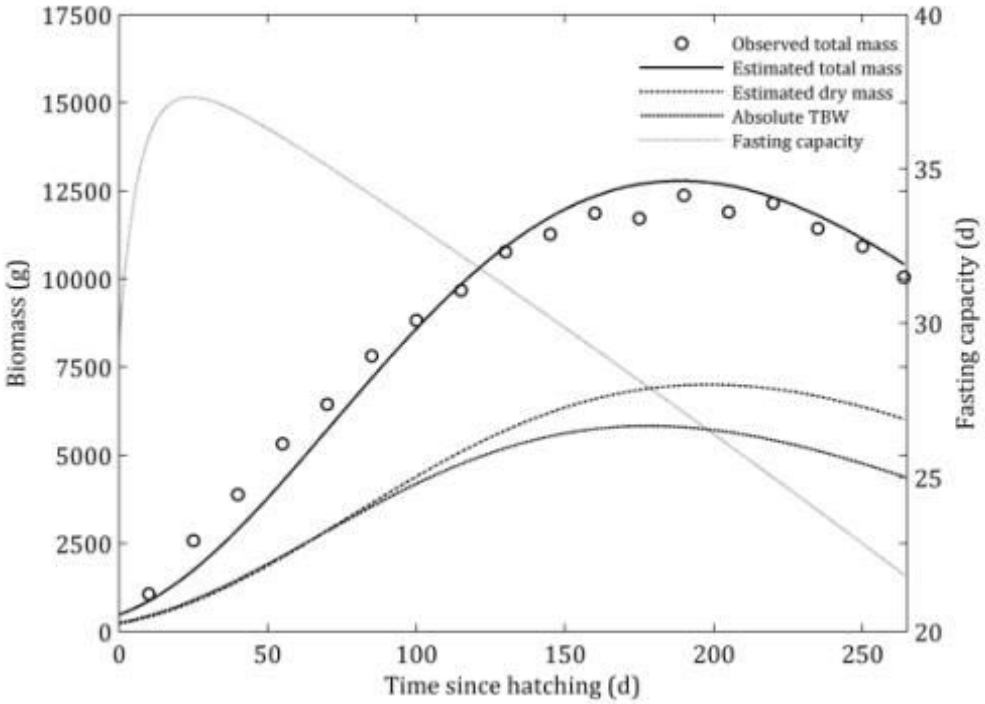

Figure 4.2 – The estimated body mass and fasting capacity before fledging. The fitted body mass growth curve, assumed absolute total body water (TBW) (left y axis) and the fasting capacity of the chick (right y axis) estimated through the application of the DEB theory. The plotted values refer to total wet weight and were measured by Lequette and Weimerskirch (1990).

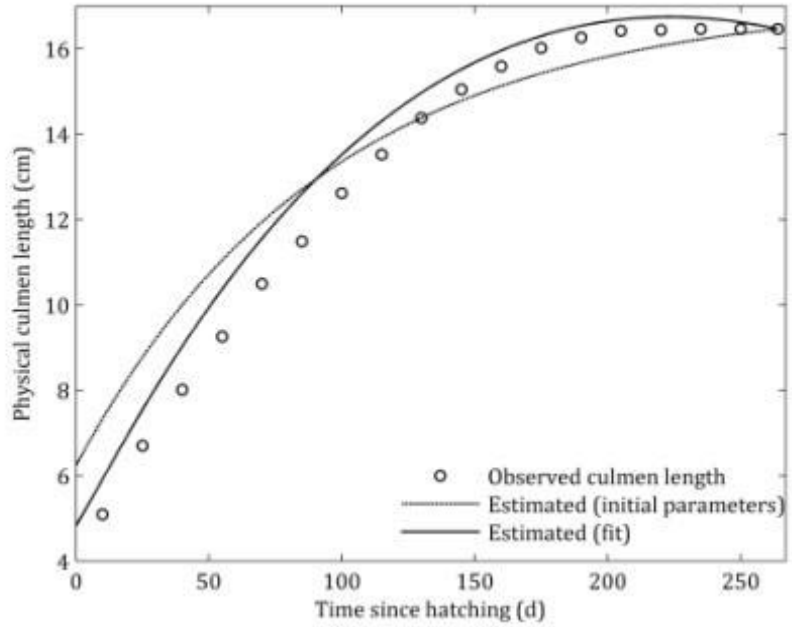

Figure 4.3 – The estimated culmen growth length before fledging. The expected culmen length von Bertalanffy growth curve estimated through the application of the DEB standard model using the initial parameters (estimated from zerovariate data) in stable feeding conditions (f = 0.8) (dashed line). The expected growth estimated using the parameter values obtained after the fit to the mass and culmen length data, with variation in total body water (TBW) and f (straight line). The plotted values were measured by Lequette and Weimerskirch (1990).

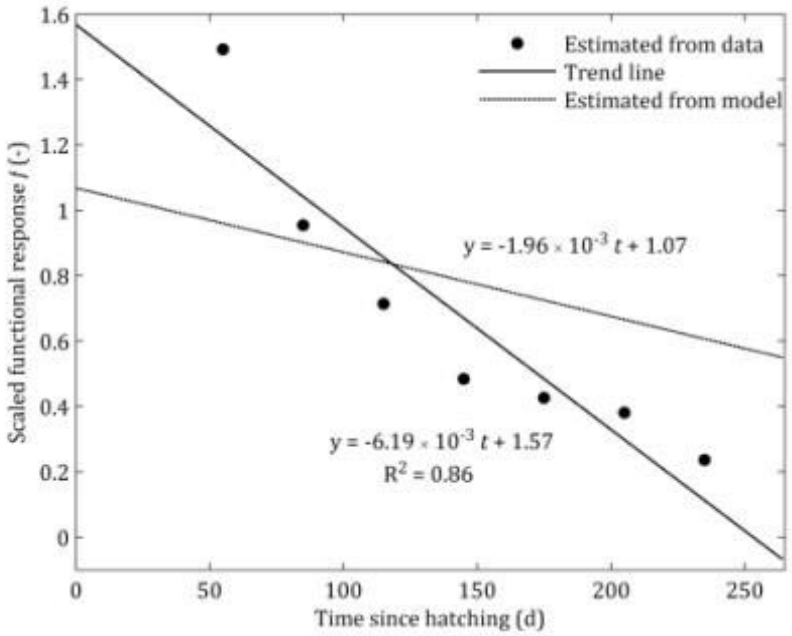

Figure 4.4 – The estimated variation in scaled functional response. The scaled functional response (f) estimated through the application of DEB theory compared to an approximation of f estimated using measurements (i.e. the ratio between the amount of food ingested per unit surface of the organism at time (t) and at the adult stage (see Table 4.7).

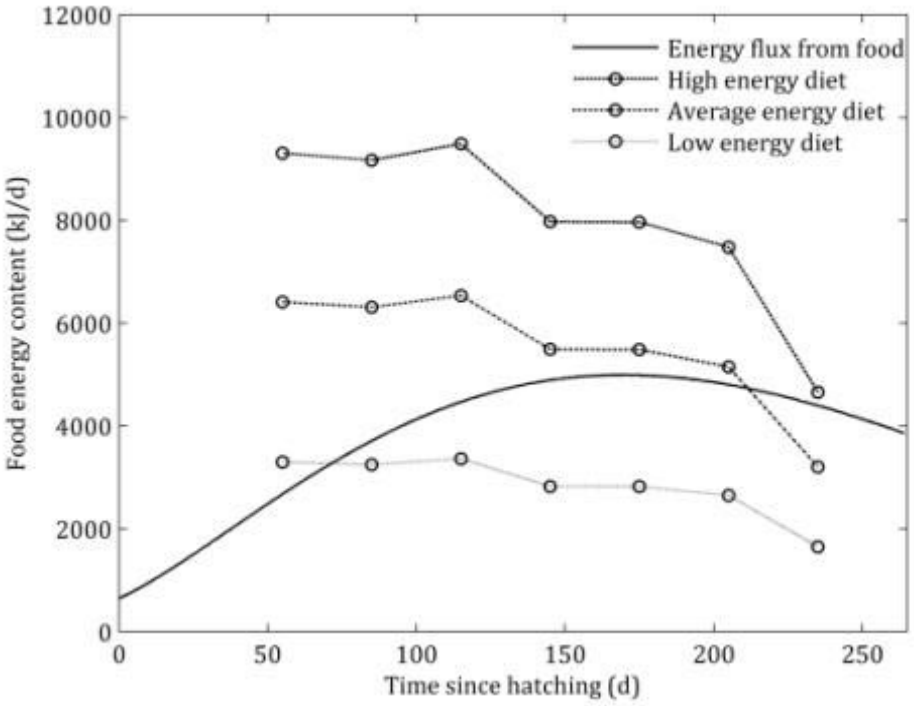

Figure 4.5 – The estimated variation in daily energy intake from food before fledging. The energy flux from the daily food ingested by the Wandering Albatross chick estimated through the application of the DEB theory. Also depicted is the estimated energy content in the average daily meal provided by progenitors (quantities measured by Weimerskirch and Lys (2000)) according to a low energy diet (100% cephalopod), an average diet (48% cephalopod + 45% fish + 7% other materials) and a high energy diet (100% fish).

4.4 Discussion

This study took into consideration our current knowledge on the biology of the Wandering Albatross, with a particular focus on the growth pattern exhibited by the chicks which includes a body mass acquisition period followed by a period of mass recession just prior to fledging. We considered the diversity of hypotheses suggested in the literature to explain the evolution of this growth pattern and a new hypothesis was formulated. Our hypothesis is based on the fact that despite sharing the same main metabolic characteristics there is a difference in the daily effort dedicated to locomotion, particularly flying, lifting off and landing on water, activities that adults perform for most of their day. Using data collected from the literature and applying the standard DEB model, we were able to test this hypothesis and confirm that a simple adjustment to the value of a parameter – the volume-specific somatic maintenance costs – subtracting the effort invested in flying from those costs, coupled with a decrease in food provisioning, is enough to estimate a growth pattern with an increase in body mass during the first few months after hatching and a decrease before fledging.

4.4.1 Data and parameter estimation

The first aspect worth discussing is the fact that with a relatively small set of life-history traits and a length growth curve it is possible to estimate values for the core parameters of the DEB standard model. However, the inclusion of the body mass growth curve and the consideration of different somatic costs for the chick allowed us to correct the set of parameter values. The main difference between the two parameter sets (Table 4.3) is in fact the $[\dot{p}_M]$ value. All the other parameters had their value only slightly adjusted, except for the maturity thresholds which had to change considering the different somatic costs and their effect.

4.4.2 Scaled functional response and body mass

One of the main results of this study is the evidence that a change in the value of the somatic maintenance costs is enough to result in an increase of body mass similar to the observed pattern. But fitting the expected body mass growth curve to previous observations required a function for f to be estimated. Our estimation of f shows a declining trend and this is consistent with the declining food provisioning observed by Weimerskirch and Lys (2000). The intersection coefficient value of our f function is greater than 1 suggesting the occurrence of a small period of overfeeding during brooding, which is consistent with observed behaviour. The slope coefficient determines that f continues to decline, reaching a value of 0.55 at fledging and suggesting mild starvation during the last weeks prior to fledging. This mild starvation would lead to the progressive depletion of reserves. Direct measurements of the amount of food provided to chicks throughout the growing period are rare in the literature. Two studies collected samples on two different months (Berrow et al., 2000; Lequette and Weimerskirch, 1990) but to our knowledge only one study collected samples throughout the breeding season at seven different times (Weimerskirch and Lys, 2000). If we were to estimate an approximation of f using that data, one possible approach would be to assess the ratio between the amount of food ingested per surface unit of the organism, at each sampled moment, and the same measurement at the adult stage. If we apply this approach using the quantities measured by Weimerskirch and Lys (2000) and the culmen length values measured by Lequette and Weimerskirch (1990) (Table 4.7), plot the results and apply a regression trend line, the equation of this line has a steeper slope than our f function and a much larger intersection coefficients (Figure 4.4). These differences highlight the precaution required if we are to assess

f solely on the basis of quantities that may not reflect the actual energy available in the food chicks ingest.

This brings us to the issue of diet composition. The amount of food provided to chicks throughout the growing period has been previously measured but those studies did not include analyses on diet composition. On the other hand, studies that focused on diet composition did not quantify the food provided to the chicks. In order to discuss our estimates on the daily energy intake of chicks and adults, we considered the diet composition obtained in six studies (Table 4.8).

The two main components of the Wandering Albatross diet are pelagic cephalopod and fish species. The rest is mainly composed of carrion (from cetaceans and other seabirds), crustaceans and jellyfish. The six considered studies reported the relative proportions of these three components but were conducted in three different archipelagos. The diet samples analyzed in Bird Island (South Georgia) are mostly composed of fish. In Île de la Possession (Crozet) and Marion (Prince Edward) islands, the diet is mostly composed of cephalopods. Diets rich in fish are usually more energetic due to the fact that fish tend to have higher percentages of fat in their body composition than cephalopods, and the calorific content of fat is typically higher than that of protein (39.7 kJ g^{-1} > 16.7 kJ g^{-1}) (Petrusewicz and Macfayden, 1971). Considering similar quantities of food, the energy content per mass unit in South Georgia should then be higher.

The South Georgia Archipelago is situated in the Atlantic Ocean while the other two archipelagos are in the Indian Ocean. However, the most representative contribution (in % of diet wet mass) to the cephalopod part of the diet is composed of the same species, the Giant Warty Squid (*Kondakovia longimana*) (Onychoteuthidae) in the three archipelagos (Ceia et al., 2012; Clarke et al., 1981; Imber, 1992; Prince and Morgan, 1987; Ridoux, 1994; Weimerskirch et al., 2005; Xavier et al., 2004). The fish part of the diet has only been studied in detail in South Georgia. Croxall et al. (1988) identified the South Georgia Icefish (*Pseudochaenichthys georgianus*) (Channichthyidae) as the main fish prey (in % of diet wet mass) but two recent studies (Ceia et al., 2012; Xavier et al., 2004) identified the Patagonian Toothfish (*Dissostichus eleginoides*) (Nototheniidae) instead.

In order to estimate the average energy content (kJ g^{-1}) of each diet we used the previously mentioned calorific content of protein and fat and the body compositions (% of body wet weight) of the Boreal Clubhook Squid, *Onychoteuthis borealijaponica* (Onychoteuthidae) (18.2% protein; 0.72% fat) (Croxall and Prince, 1982) and of the Patagonian Toothfish (15.65% protein; 17.06% fat). The composition of the Giant Warty squid was unavailable. Using these values, we estimated an energy content of 3.33 kJ g^{-1} for the cephalopod part of the diet, and of 9.38 kJ g^{-1} for the fish part of the diet. We also considered the rest of the diet to have a composition similar to fish. The average energy content per mass unit of the South Georgian meals is indeed expected to be higher than in the Indian Ocean archipelagos (Table 4.8). The average diet, considering the six studies, would be constituted by about 48% of cephalopods, 45% of fish and 7% of other materials, and would have an average energy content of 6.46 kJ g^{-1}.

In order to contextualize the flux of energy from food that we estimated to occur, we plotted those values (Figure 4.5), comparing that curve with the energy that would be available in the average daily food provided by progenitors considering: a) the quantities measured by Weimerskirch and Lys (2000); b) the energy content values we estimated, and c) the lowest

energetic diet (100% cephalopods), our estimated average diet and the most energetic diet (100% fish).

For the observed growth pattern to emerge, our estimated flux of energy from food would be expected to increase during the first couple of months (brooding included), but could be fulfilled even with a low energy diet (mostly cephalopods), if quantities would be similar to those measured by Weimerskirch and Lys (2000). According to these same authors this is the period when progenitors are losing weight, performing a higher proportion of short trips and catching prey near the breeding sites at a time when cephalopods could be available in large quantities. This is precisely the period when Weimerskirch et al. (2005) collected the diet samples that had the highest proportion of cephalopods. Other studies that measured quantities of food provided in May (Berrow et al., 2000; Lequette and Weimerskirch, 1990) reported averaged daily values inferior to those observed by Weimerskirch and Lys (2000) which could be explained if a higher proportion of fish was already being collected. It is during brooding that we estimated the fasting capacity to increase to about 37 d and it remains close to that during these two first months.

From then on, our estimated energy flux converges towards an average diet, with higher energy content and a progressively higher proportion of fish. According to Weimerskirch and Lys (2000) this is the period when progenitors are able to recover their own body condition, which would probably benefit from a diet rich in fat and protein. This average diet profile seems adequate from July (130 d since hatching) to September (205 d). We estimate fasting capacity to be between 26 and 31 d, an interval that is well above the average foraging trip duration registered in 1999 (13.7 d) and 2000 (7.8 d) by Xavier et al. (2004). Fasting capacities above the expected stochasticity in fasting periods have already been estimated for other seabirds such as the Cape Gannet (*Morus capensis*) (Navarro, 1992) and the Northern Fulmar (*Fulmarus glacialis*) (Phillips and Hamer, 1999). However, Xavier et al. (2004) observed trip durations in Wandering Albatrosses ranging from 0.9 d to 36.9 d (although trips spanning about a month seem to be less common). This means that it is still possible for the chick to go through short and irregular mild starvation periods from which he recovers and reassumes normal growth throughout the breeding season. After that, when the frequency of visits by progenitors decreases and our estimated fasting capacity is similar to adult values (22 d ~ 25 d), our results seem to suggest that the energy required should have to come from energy rich meals (mostly composed of fish) considering the quantities measured by Weimerskirch and Lys (2000). Samples taken mostly during this time period revealed high proportions of cephalopods once again (Cooper, 1978; Ridoux, 1994) but only refer to the Indian Ocean archipelagos where the main squid prey may still be relatively available. This is the period when protein (available in cephalopods and fish) is necessary for feather growth but chicks are already losing weight (probably reserve + water), and therefore the variation in the relative proportion of fish, in the few meals provided, helps to determine the rate at which the chick loses weight and fledging becomes viable.

The expected energy available in the daily food ingested by adults (3,646.83 kJ d^{-1}) would correspond to 1.1 kg d^{-1} of food in a low energy diet, 0.6 kg d^{-1} in an average diet or 0.4 kg d^{-1} in a high energy diet. From measurements taken by Weimerskirch and Wilson (1992), it is possible to estimate daily food quantities ingested by incubating adults that go from about 1 kg to 2.6 kg. Salamolard and Weimerskirch (1993) estimated 2 kg d^{-1} during incubation but 1.45 kg d^{-1} when chicks are about to fledge. Our estimated values are in the order of what has been previously estimated and measured, but somewhat below those averages, which suggests higher proportions of cephalopods are probably the typical diet when adults are foraging for their own nutritional requirements. Our estimates would also be higher if we would consider

lower digestive efficiencies in the adult stage (κ_X < 0.8). For instance, if κ_X = 0.5, the same amount of expected daily energy intake would correspond to 1.8 kg d^{-1} in a low energy diet. Variation in the diet composition and digestive efficiency at different times (and for different kinds of prey) is enough for measurements taken in the field to differ considerably.

4.4.3 Metabolic rates

Our estimates for the FMR (4.29 W kg^{-1}) and the RMR (2.87 W kg^{-1}) are close to the values obtained experimentally (Table 4.6). The diversity of techniques previously used include estimates of metabolic water production derived from water influx rate (WIR) and the injection of doubly labelled water (DLW) converted to CO_2 production, energy expenditure from mass loss (ML) and oxygen consumption ($\dot{V}O_2$) and heart rate measurements calibrated from oxygen consumption values. Our estimate of FMR is just 4% below the average (4.48 W kg^{-1}) and 8% above the lowest estimation (3.94 W kg^{-1}) which was obtained through the conversion of CO_2 production measured from a DLW influx rate (Arnould et al., 1996). Therefore our results suggest that applying the DEB standard model using a short set of data is enough to provide an estimated value for FMR which is almost equal to the average values obtained by using isotope injection techniques. These techniques have been characterized as useful to study the energy expenditure of free-ranging animals (Shaffer, 2011).

In most studies the values presented for basal metabolic rate (BMR) actually correspond to RMR, as it is difficult to isolate the energy being expended exclusively with metabolic processes involving no movement or stress related discrepancies. Our estimate for RMR was therefore compared to values previously published as BMR estimates and it is just 6% above the average (2.7 W kg^{-1}). In fact it is very similar to the values obtained through measurements of $\dot{V}O_2$ by Brown and Adams (1984). Our estimate is below the values obtained from ML measurements and WIR analysis. Both methods evaluate the water flux and infer energy expenditure from the catabolism of body mass. By allowing some movement beyond resting, these methods may overestimate RMR.

Our estimates for FMR and RMR are very close to the averages obtained in the field but did not require the application of any invasive technique. Nevertheless, further studying with other bird species will help to clarify the utility of DEB for this purpose on a broader scale.

Table 4.6 – Comparison between the resting metabolic rate (RMR) and field metabolic rate (FMR) values obtained experimentally in previous studies and the values estimated in the present study through the application of DEB theory (WIR – water influx rate; ML – mass loss rate; $\dot{V}O_2$ – dioxygen consumption; DLW – $\dot{V}CO_2$ – doubly labelled water converted to CO_2 production; HR – $\dot{V}O_2$ – heart rate calibrated from dioxygen consumption).

Method	RMR (W kg^{-1})	FMR (W kg^{-1})	Reference
WIR	3.99	-	Shaffer et al. (2001b)
ML	3.21	-	Shaffer et al. (2001b)
$\dot{V}O_2$	2.86	-	Brown and Adams (1984)
$\dot{V}O_2$	2.50	-	Brown and Adams (1984)
DLW – $\dot{V}CO_2$	1.96	-	Shaffer et al. (2001b)
HR – $\dot{V}O_2$	1.70	-	Weimerskirch et al. (2002)
DLW – $\dot{V}CO_2$	-	4.90	Shaffer et al. (2001a)
DLW – $\dot{V}CO_2$	-	4.59	Adams et al. (1986)
DLW – $\dot{V}CO_2$	-	3.94	Arnould et al. (1996)
Average	2.70	4.48	-
This study	2.87	4.29	-

Table 4.7 – Comparison between the scaled functional response (f) expected values, obtained through the estimated function after applying DEB theory and fitting observed body mass variation, and the ratio between the amount of food ingested per surface unit of the organism, at each sampled moment (X/L^2), and the same measurement at the adult stage (X_∞/L_∞^2) ([1] Weimerskirch and Lys (2000); [2] Lequette and Weimerskirch (1990); [3] average daily meal size for adults measured by Weimerskirch et al. (1994)).

Age (d)	[1] Food provided (X) (g d^{-1})	[2] Culmen length (cm)	$\frac{X}{L^2}$ (g d^{-1} cm^{-2})	$\frac{X/L^2}{X_\infty/L_\infty^2}$ (-)	f (-)
55	991.83	9.26	11.57	1.49	0.96
85	977.00	11.49	7.4	0.95	0.9
115	1011.23	13.52	5.53	0.71	0.84
145	849.78	15.05	3.75	0.48	0.78
175	848.70	16.02	3.31	0.43	0.72
205	796.68	16.42	2.95	0.38	0.66
235	496.14	16.46	1.83	0.24	0.60
Adult [3]	2100.00	16.46	7.75	1	0.8

Table 4.8 – The relative diet compositions provided by Wandering Albatrosses to their chicks, measured in six different studies ([1] Weimerskirch et al., 2005; [2] Xavier et al., 2004; [3] Prince and Morgan, 1987; [4] Ceia et al., 2012; [5] Ridoux, 1994; [6] Cooper et al., 1992). Weimerskirch et al. (2005) sampling period included the incubation period. Samples were taken from the stomachs of adults or chicks depending on the study. The energy content was estimated based on the calorific contents of Onychoteuthidae squid and Nototheniidae fish species.

Location	Time period	Cephalopods (%)	Fish (%)	Other (%)	Samples	Energy content (kJ g^{-1})	Reference
Île de la Possession (Crozet)	February – April	71	22	7	Chicks (n = 64)	5.08	1
Bird Island (South Georgia)	May – August	42.1	53.1	4.8	Adults (n = 18)	6.83	2
Bird Island	May – August	11.3	84.3	4.4	Adults (n =20)	8.7	2
Bird Island	May – September	35	41.5	19	Chicks (n = 80)	6.99	3
Bird Island	May – October	38.4	59.4	2.2	Adults (n = 35)	7.06	4
Île de la Possession	August – October	76.7	14.9	8.4	Chicks (n = 37)	4.74	5
Marion Island (Prince Edward)	June – December	58.6	36.5	4.9	Chicks (n = 50)	5.83	6
Average	-	48	45	7		6.46	-

4.5 Conclusions

Growth patterns with energy accumulation in reserve and body mass recession before fledging may result from different reasons in different species. Leach's Storm Petrels (*Oceanodroma leucorhoa*) accumulate fat but deplete part of these reserves before fledging (Mauck and Ricklefs, 2005). These reserves were partly useful during development, and this has been usually considered as a probable way to overcome the risk of stochastic variation in food provisioning by the progenitors (Mauck and Ricklefs, 2005; Ricklefs and Schew, 1994). The remaining reserves may still be useful to increase the chances of survival during the initial critical period after fledging. In the Northern Fulmar, recession before fledging results from a decline in TBW and lean dry mass of some organs (liver, kidney and gut) (Phillips and Hamer, 2000, 1999) but fledglings have more fat than adults. In the Cape Gannet there is a decline in TBW, fat and lipid-free dry matter (Navarro, 1992). After fledging, body mass keeps declining to adult levels mostly due to fat and marginally to TBW. For these two species the reserves seem to be mostly useful after fledging (especially in the case of the Northern Fulmar).

In DEB theory, the reserve is necessary to include metabolic memory, i.e. to smooth out fluctuations in food availability (Kooijman, 2010a). According to the hypothesis we tested, the possibility that chicks and adults share the main metabolic traits that regulate assimilation and growth, but differ in the relative effort dedicated to locomotion, is enough to allow for an energy surplus to be stored since hatching, in the reserve. The existence of this growth pattern may have not been driven by stochasticity as some studies suggested (Lack, 1968; Ricklefs and Schew, 1994; Ricklefs, 1990) and instead be the result of physiological processes as Phillips and Hamer (2000) proposed. Our results suggest that feeding chicks generously during the first months of development is enough to quickly raise their fasting capacity up to levels above the average fasting period, as it has been observed in other species (Navarro, 1992; Phillips and Hamer, 1999). The reserves are then sufficient to help sustain the increasing energetic requirements of the chick even when a decline in food provisioning and a changing diet composition are taking place and part of the reserves will still be available for the post-fledging period. It seems plausible that for birds breeding in remote places and foraging over large areas, energy reserves will always be at least partially useful to reduce the risk from stochasticity in food provisioning during chick development. In a similar way, this growth pattern may have not been driven by higher energy-demanding periods before fledging as pointed out in some studies (Obst and Nagy, 1993; Reid et al., 2000; Ricklefs, 1979b) or learning periods after fledging (Perrins et al., 1973; Phillips and Hamer, 1999), but the availability of reserves would be positively selected if the diet available is energetically poorer and feeding frequency is decreasing (but feathers are still growing or foraging skills are still to be learned).

Our results also suggest that the decline in food provisioning and related decrease in daily energy intake is enough to explain reserve depletion and body mass recession in Wandering Albatrosses. This is different from the observations of Mauck and Ricklefs (2005) regarding Leach's Storm Petrels whereby the completion of structural growth works as an endogenous trigger that initiates a period when the chick refuses most meals and decreases in mass. Based in our study, we suggest that in semi-altricial species, such as the Wandering Albatross, different behavioural profiles in terms of locomotion effort, before and after fledging, may provide chicks with an energy surplus that can be stored in reserve. When colonizing remote breeding sites, these reserves would be beneficial, constituting 'energy-sinks', covering stochasticity related to feeding strategies and increasing the chances of survival after fledging, when flying and foraging skills are being learned. In other bird species with very different

locomotion efforts occurring in the chick and adult stages, we can expect growth patterns similar to that of the Wandering Albatross, to be exhibited.

The application of the DEB standard model to bird species may help to understand the diversity of growth patterns observed in this group. The approach presented in this study also shows that through DEB theory it is possible to use a small set of life-history traits coupled with growth data and reliably estimate a variety of other traits related to the energetics of birds, such as food availability, daily energy intake, fasting capacities and standard metabolic rates.

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Abstract

Biodiversity is declining worldwide at a rate unprecedented in the recent era and this trend is expected to persist throughout the century. There is a broad consensus that in the absence of conservation action, biodiversity will continue to be lost, threatening the stability, functioning and sustainability of ecosystems and increasing the likelihood of ecological unexpected events with negative impacts on human well-being.

Several indicators have been used to document this declining trend, including those focusing on the mean species abundance and genetic diversity. There is also evidence that the distribution of species on Earth is becoming more homogenous and a significant portion of well-studied higher taxonomic groups are currently threatened with extinction. One of these groups includes all of the currently living bird species, which have been grouped in the biological class Aves, according to Linnaean taxonomy, and in the crown group Neornithes, according to modern phylogenetic taxonomy.

The main causes for biodiversity decline emerge from human activities and include the conversion of natural habitats, overexploitation or climate change, among several others. Globally, the most significant threat for bird species is the conversion of natural habitats to agricultural land. The impact of invasive alien species on many bird species is also well documented. However, there is high uncertainty regarding the direct and indirect ways through which climate change may be affecting birds. Recent empirical studies, using data collected over long periods of time, suggested that the effects of climate change on birds may lead to shifts in their potential distribution ranges or to actual changes in body size (mass and length). Some studies documented increases in body size while other studies described size declining trends throughout the last decades.

Several authors have been highlighting the need to develop theoretical models that would relate metabolism to body size in order to assess the vulnerability of species under the effect of climate change. These models would also help to identify the proximate mechanisms that ultimately may determine size shifts. Recently, this need has also been stressed in order to allow the creation of general ecosystem models (GEM).

Generally speaking, metabolism and the mechanisms of energy intake, assimilation, allocation and use, have rarely been explored and modelled for conservation purposes. Within the study of the life history of organisms this has also been the case. Research based on life history theory has been mostly aiming at the characterization of global patterns and of exogenous and endogenous drivers of life history variation.

Studies searching for endogenous drivers of variation have been mostly focused on phylogeny. The existence of relevant processes taking place at the physiological and metabolic scales has been harder to study. Previous attempts to account for the metabolic costs associated with different life history traits focused mostly on reproduction. Few studies have tried to assess the trade-offs between reproduction and assimilation, growth, and other biological properties. However, in the last two decades, several authors stressed the need to research the existence of proximate mechanisms of variation in trait expression, mediating the effect of environmental selective pressures on life history traits and constraining their variation.

Therefore, the need to develop explicit, mechanistic and individual-based models, linking the constraints of metabolism to life history evolution, in order to understand the evolution of life history strategies and to improve our future conservation strategies, seems to be paramount.

In this context, the study of avian metabolism and energetics emerges as a field of considerable relevance. Different techniques are currently used for the study of avian energetics but most rely on experimentation. Theoretical modelling has been mostly performed through the application of allometry and Static Energy Budgets (SEB), which have several limitations. Alternatively, Dynamic Energy Budgets (DEB) follow how energy fluxes change during the life cycle of organisms. Currently, the DEB theory is the only metabolic theory that uses these models and complies with the Laws of Thermodynamics, unifying traits that are common to all organisms and linking different levels of biological organisation.

The main hypothesis of this thesis considered that the properties represented by DEB theory's parameters and functions could correspond to the proximate mechanisms that mediate the effect of external selective pressures on the evolution of birds. Ultimately, these endogenous properties, and their respective diversity, would constrain and determine the diversity and the trade-offs observed in the life history traits of modern bird species.

For the purpose of testing this hypothesis, the standard model of the DEB theory was applied in order to model the life cycles of a representative collection of bird species. This collection corresponds to a sample of the existing diversity in terms of phylogeny, distribution and life history traits of modern birds. The input data consisted of single-point information regarding different life history traits related to growth, development thresholds and reproduction, as well as of growth curves, collected for every species of the collection.

The parameterization procedure was undertaken using the covariation method, providing estimates for the core DEB parameters. The estimated DEB parameter sets allowed for accurate predictions of known life history traits and the von Bertalanffy growth pattern provided a very good adjustment for most species.

The results allowed us to observe that the allocation of energy to somatic growth and maintenance is particularly high in birds, with a very low coefficient of variation, suggesting a high degree of phylogenetic inertia throughout the evolution of birds. Among other properties, birds seem to be characterized by parameter sets that promote rapid growth rates, prioritizing the development of soma. Some DEB parameters and functions that are not expected to scale with body size exhibited patterns suggesting otherwise. The diversity and scatter of values observed for several parameters may offer the necessary adaptive plasticity for birds to adjust to current global change scenarios.

Through the ecological characterization of the sampled bird species, it was also possible to test a set of hypotheses relating the physiology of birds to their respective ecology and behaviour. Several theories and hypotheses proposed in the literature concerning specific aspects of the life history of birds were also discussed. Apparent trade-offs, between different life history traits, were shown to emerge from metabolic constraints.

The patterns observed for many primary and compound DEB parameters were significantly explained by body size. Factors such as the hatchling development type, within the altricial-to-precocial spectrum, or the capacity to fly and migrate, were also particularly relevant for that purpose. Strong positive correlations between several DEB parameters were consistent with the waste-to-hurry strategy, with somatic maintenance costs increasing as a response to

increased growth rates, ultimately determining the evolution of altriciality from earlier, precocial ancestors.

It was also possible to estimate that the hatchlings of precocial species exhibit higher values of maturity per unit of dry mass at birth than the hatchlings of altricial species. If we consider the relative investment in maturation as an indicator of complexity, then these results support the thesis of higher complexity at birth in precocial birds.

Finally, the case study of the Wandering Albatross (*Diomedea exulans*) is presented as an example of how food availability may determine rare and extreme growth patterns in highly constrained environments. The application of DEB theory allowed for a thermodynamically explicit model to be developed for this endangered species, testing one hypothesis explaining the observed growth pattern and providing other useful metabolic properties, such as the expected fasting capacity and the daily energy intake of hatchlings and adults.

Keywords

Birds; Dynamic Energy Budget (DEB) theory; conservation; life history evolution; life cycle; metabolism; energy; parameter estimation; Wandering Albatross; *Diomedea exulans*.

Samenvatting

Biodiversiteit is met een ongekende snelheid wereldwijd aan het verminderen en deze trend zal, naar verwachting, nog de gehele eeuw doorgaan. Er is een breed draagvlak voor de mening dat, in afwezigheid van conserverings maatregelen, biodiversiteit voortdurend zal afnemen en daarmee worden de stabiliteit, het funcktioneren en de duurzaamheid van ecosystemen bedreigd en bestaat een verhoogde kans dat onverwachte ecologische gebeurtenissen negatieve gevolgen zullen hebben voor het menselijk welzijn.

Verschillende indicatoren zijn gebruikt om de biodiversiteits-afname te documenteren, zoals gemiddelde abundantie van soorten en genetische diversiteit. Het is duidelijk geworden dat de verspreiding van soorten op aarde meer homogeen is geworden en dat een flink deel van de goed-bestudeerde hogere taxomomische groepen nu met uitsterven bedreigd worden. Een van die groepen bestaat uit vogels van alle soorten, zij worden tot de klasse der Aves gerekend volgens de taxonomie van Linneus, en tot de kroongroep Neornithes, volgens de moderne fylogenetische klassificatie.

De belangrijkste oorzaken voor het verlies van biodiversiteit zijn, ondermeer, het verlies van natuurlijk habitat, over-exploitatie en klimaatsverandering. Voor vogels is de eerste oorzaak het belangrijkste, door omzetting naar landbouwgrond. Effecten van geintroduceerde soorten is een andere bekende oorzaak. Er is onzekerheid over het belang van klimaatsverandering voor vogels, direct alsmede indirect. Recente empirische studies, gebaseerd op data die over een lange pweriode verzameld zijn, suggereren dat klimaatsverandering kan leiden tot verschuivingen in het potentieel verspreidingsgebied van soorten en veranderingen in de grootte van individuen (lengte, massa). Sommige studies laten een toename, andere een afname zien over de laatste decennia.

Verschillende auteurs wijzen op de noodzaak theoretische modellen te ontwikkelen voor hoe het metabolisme afhangt van de lichaamsgrootte, om zodoende de kwetsbaarsheid van soorten voor klimaatsveranderingen te kunnen voorspellen. Deze modellen zouden ook gebruikt kunnen worden om direct meachismen op te sporen die uiteindelijk de lichaamsgrootte bepalen. Nog onlangs is deze noodzaak nogmaals benadrukt om algemene ecosysteem modellen te maken.

Algemeen gesproken zijn het metabolisme en de mechanismen van energie inname, allocatie (= toewijzing) en gebruik nog maar zelden bestudeerd en gemodelleerd voor conserverings-doeleinden. Dit is ook het geval binnen de context van de natuurlijke historie van organismen. De theorie van natuurlijke historie houdt zich vooral bezig met ruwe patronen en interne en externe factoren die variatie in natuurlijke historie bepalen.

Studies naar interne factoren die variatie bepalen zijn sterk gericht geweest op de fylogenie (= afstammingsleer). Relevante processen op fysiologische en metabole schaal bleken moeilijker te bestuderen. Tot nu toe lag de belangstelling vooral bij de metabole kosten van de verschillende natuurhistorische eigenschappen en hun effect op reproductie. Weinig studies beschouwden de interacties tussen de verschillende processen, zoals reproductie, assimilatie en groei. De laatste twee decennia, echter, hebben verschillende auteuren de noodzaak benadrukt voor onderzoek naar deze interacties, en hoe selectie processen de variatie inperken. Er is dus blijkbaar een grote behoefte aan expliciete, op individuen gebaseerde,

mechanische modellen die randvoorwaarden van het metabolisme knopen aan stategieen in natuurlijke historie om toekomstige conserverings strategien te bepalen.

De studie naar het metabolisme en de energetica van vogels komt in deze context tevoorschijn als een gebied met grote relavantie. Verschillende technieken die voor de studie van vogel energetica gebruikt worden leunen sterk op experimenten. Theoretische modellen betreffen vooral toepassingen van allometrie en zogenaamde Statische Energie Budgetten, die verschillende beperkingen met zich mee brengen. Dynamische Energie Budgetten (DEBs) volgen echter energie stromen gedurende de hele levenscyclus van organismen. DEB theorie is op dit moment de enige metabole theorie die van DEBs gebruik maken, recht doet aan de wetten van de theromodynamica, eigenschappen vereeningen die alle organsimen gemeenschappijk hebben en de verschillende biologische organisatie niveaus met elkaar verbinden.

De belangrijkste vooronderstelling van dit proefschrift is dat de eigenschappen, die door parameter waarden gerepresenteerd worden, te maken zou kunnen hebben met mechanismen die de effecten beinvloeden van externe selectie druk op de evolutie van vogelsoorten. Uiteindelijk zouden deze endogene eigenschappen de biodiversiteit bepalen, alsmede de interaktie tussen natuurhistorische eigenschappen van heden-ten-daagse vogels.

Om deze vooronderstelling te toetsen is het standaard DEB model toegepast op de levencyclus van een verzameling representatieve vogel-soorten. Deze verzameling is representatief in termen van afstamming (alle vogel orden zijn vertegenwoordigd), verspreiding en natuurhistorische eigenschappen. De verzamelde data bevat informatie over groei, ontwikkeling, reproductie en veroudering en omvat een groei-curve voor elke soort.

De covariatie methode is gebruikt voor de schatting van de DEB parameters. Deze waarden maken het mogelijk natuurhistorische eigenschappen nauwkeurig te voorspellen. Het von Bertalanffy groei model, dat door het DEB model wordt geimpliceerd, bleek voor de meeste soorten inderdaad zeer goed toepasbaar.

De resultaten laten zien dat vogels relatief veel energie besteden aan somatische groei en onderhoud, met een erg lage variatie coefficient, hetgeen in hoge mate evolutionair bepaald lijkt te zijn. Dit stelt ze in staat snel te groeien en ze geven deze groei prioriteit boven reproductie. Sommige parameter waarden, waarvan niet verwacht werd dat ze van de uiteindelijke lichaams-grootte af zouden hangen, blijken dat toch te doen. De patronen die sommige parameters laten zien zouden kunnen wijzen of adaptieve plasticiteit die nodig is om grootschalige veranderingen in de omgeving de baas te kunnen.

Sommige patronen in parameter waarden konden begrepen worden door de oecologie en het gedrag van de soorten erbij te betrekken. Het proefschrift bespreekt ook enkele hyposthesen die in de literatuur zijn voorgesteld met betrekking tot de natuurlijke historie van vogels. Interakties tussen natuurhistorische eigenschappen, zoals in de literatuur omschreven, blijken het gevolg te zijn van interacties van metabole eigenschappen en zijn daardoor nu beter begrepen.

Veel patronen in primaire en samengestelde DEB parameters konden geklaard worden door de uiteindelijk lichaamsgrootte. Het type van uit-het-ei-komen, het vermogen om te vliegen en te migreren en de positie in het zogenaamde altricial-precocial spectrum, bleken met parameter waarden samen te hangen. ("Altricial" betekent "vroeg-geboren", naakt en blind; "precocial" betekent "laat-geboren", klaar om er vandoor te gaan.) Sterke correlaties tussen verschillende DEB parameters bleken consistent met de verspil-om-te-haasten (wast-to-hurry) stategie,

daarbij het specifieke somatisch onderhoud wordt verhoogd om de groei te stimuleren. (Dit lijkt tegenstrijdig maar is het niet in een DEB context.) Dit heeft evolutionair geleid tot de ontwikkeling van de alticial strategie uit voorouders die de precocial strategie volgden.

Niet onverwacht blijken precocial soorten bij geboorte een hogere maturiteit (= graad van ontwikkeling) per gewicht te hebben dan altricial soorten. Dit lijkt een open deur, maar dit soort zaken zijn niet eenvoudig uit modellen te halen omdat de realitiet veel complexer is dan welk model danook. Bovendien kunnen we de mate van alticial-zijn kwantitatief uitdrukken, dat voorheen niet mogeliojk was. Als de investering in ontwikkeling (maturiteit) een maat is voor complexiteit, dan zijn precoxial soorten dus complexer dan altricial soorten.

Tenslotte beschrijft dit proefschrift de casus van de reuzenalbatros (Diomedea exulans) als voorbeeld van hoe voedsel beschikbaarheid de groei beinvloedt in veel-eisende omgevingen. Deze toepassing van DEB theory illustreert haar toepasbaarheid in het geval van een bedreigde diersoort. De theorie wordt hier gebruikt om een hypothese te toetsen omtrent een waargenomen groei-patroon, en ze maakt bruikbare metabole eigenschappen zichtbaar, zoals het vermogen om met hongering om te gaan en het dagelijks energie-opname van het kuiken versus die van de adult.

Trefwoorden

Vogelstand; Dynamisch Energie Budget (DEB) theorie; behoud; levensgeschiedenis evolutie; levenscyclus; metabolisme; energie; parameterschatting; Omzwerving Albatros; *Diomedea exulans*.

Resumo

A biodiversidade mundial encontra-se em declínio a um ritmo que não encontra precedentes na era recente e estima-se que esta tendência venha a persistir ao longo do século. Existe um claro consenso de que, na ausência de acção conservacionista, a biodiversidade irá continuar em declínio, ameaçando a estabilidade, o funcionamento e a sustentabilidade dos ecossistemas e aumentando a probabilidade de eventos ecológicos inesperados com impactos negativos no bem-estar humano.

Vários indicadores têm sido usados para documentar esta tendência de declínio, incluindo aqueles que medem a riqueza específica média e a diversidade genética. Existem também evidências de que a distribuição das espécies na Terra está a ficar mais homogénea e de que um número significativo de grupos taxonómicos bem estudados estão actualmente ameaçados de extinção. Um destes grupos inclui todas as espécies de ave que vivem actualmente e que foram agrupadas na classe Aves, de acordo com a taxonomia de Lineu, e no grupo coroa Neornithes, de acordo com a moderna taxonomia filogenética.

As principais causas para o declínio da biodiversidade emergem de actividades humanas e incluem a conversão dos *habitat* naturais, a sobre-exploração ou as alterações climáticas, entre diversas outras. Globalmente, a ameaça mais significativa para as aves é a transformação do *habitat* natural em terreno agrícola. O impacto que as espécies exóticas invasoras têm sobre muitas espécies de ave, está também bastante documentado. Contudo, existe grande incerteza em relação às formas directas e indirectas pelas quais as alterações climáticas podem estar a afectar as aves. Estudos empíricos recentes, utilizando dados recolhidos durante longos de períodos de tempo, sugeriram que os efeitos das alterações climáticas nas aves podem levar a alterações nas respectivas áreas de distribuição ou a alterações do tamanho do corpo (massa e comprimento). Alguns estudos apresentaram aumentos do tamanho do corpo enquanto outros estudos descreveram tendências de declínio do tamanho do corpo ao longo das últimas décadas.

Vários autores têm destacado a necessidade de desenvolver modelos teóricos que relacionem o metabolismo e o tamanho do corpo de forma a estimar a vulnerabilidade das espécies sob o efeito das alterações climáticas. Estes modelos ajudariam também a identificar os mecanismos proximais que, em última análise, podem determinar as alterações de tamanho. Recentemente, esta necessidade tem sido também salientada de forma a permitir a criação de modelos gerais dos ecossistemas (GEM).

Em termos globais, o metabolismo e os mecanismos de aquisição, assimilação, alocação e uso da energia, raramente têm sido explorados e modelados para fins conservacionistas. No estudo da história de vida dos organismos também tem sido este o caso. A investigação baseada na teoria da história de vida tem procurado sobretudo caracterizar os padrões globais e os motores exógenos e endógenos que promovem a variação das histórias de vida.

Os estudos que procuram os motores endógenos de variação têm-se focado sobretudo na filogenia. A existência de processos relevantes às escalas fisiológica ou metabólica tem-se demonstrado mais difícil de averiguar. Tentativas anteriores de quantificação dos custos metabólicos associados a diferentes características de história de vida focaram-se sobretudo na reprodução. Poucos estudos procuraram estimar os compromissos entre reprodução,

assimilação, crescimento e outras propriedades biológicas. Contudo, nas últimas duas décadas, vários autores sublinharam a necessidade de investigar a existência de mecanismos proximais de variação na expressão destas características, mediando o efeito das pressões selectivas de natureza ambiental nas características de história de vida e constrangendo a respectiva variação.

Neste sentido, a necessidade de desenvolver modelos baseados no indivíduo, explícitos e mecanísticos, relacionando os constrangimentos do metabolismo com a evolução das histórias de vida, de forma a compreender a evolução das estratégias de vida e a melhorar as nossas estratégias de conservação futuras, parece ser substancial.

Neste contexto, o estudo do metabolismo e da energética das aves emerge como uma área de considerável relevância. Diferentes técnicas são actualmente utilizadas para o estudo da energética das aves mas a maioria baseia-se na experimentação. A modelação teórica tem sido utilizada sobretudo através da aplicação da alometria e de *Static Energy Budgets* (SEB), técnicas que dispõem de diversas limitações. Em alternativa, os *Dynamic Energy Budgets* (DEB) acompanham a forma como os fluxos de energia se alteram durante o ciclo de vida dos organismos. Na actualidade, a teoria DEB é a única teoria metabólica que utiliza estes modelos e cumpre com as Leis da Termodinâmica, unificando características que são comuns a todos os organismos e relacionando diferentes níveis de organização biológica.

A hipótese principal desta tese considera que as propriedades representadas pelos parâmetros e funções da teoria DEB poderiam corresponder aos mecanismos proximais que medeiam o efeito das pressões selectivas externas na evolução das aves. Em última análise, estas propriedades endógenas, e a respectiva diversidade, iriam constranger e determinar a diversidade e os compromissos observados nas características de história de vida das espécies de ave modernas.

Para testar esta hipótese, o modelo padrão da teoria DEB foi aplicado de forma a modelar os ciclos de vida de uma colecção representativa de espécies de ave. Esta colecção corresponde a uma amostra da diversidade existente em termos de filogenia, distribuição e características de história de vida das aves modernas. Os dados de entrada incluíram informação individual sobre diversas características de história de vida relacionadas com o crescimento, as etapas do desenvolvimento e a reprodução, bem como também curvas de crescimento, e foram recolhidos para todas as espécies da colecção.

A parametrização foi levada a cabo através do método da covariação, providenciando estimativas para os parâmetros DEB principais. Os conjuntos de parâmetros DEB estimados permitiram prever, com precisão, características de história de vida conhecidas, e o padrão de crescimento de von Bertalanffy permitiu um ajuste muito bom para a maioria das espécies.

Através dos resultados obtidos, foi possível observar que a alocação de energia para o crescimento somático e manutenção é particularmente elevado nas aves, com um coeficiente de variação muito reduzido, sugerindo um grau elevado de inércia filogenética através da evolução das aves. Entre outras propriedades, as aves parecem ser caracterizadas por conjuntos de parâmetros que promovem taxas de crescimento elevadas, atribuindo prioridade ao desenvolvimento somático. Alguns parâmetros e funções DEB cuja independência do tamanho do corpo é esperada exibiram padrões sugerindo o contrário. A diversidade e dispersão dos valores observados para vários parâmetros podem oferecer às aves a plasticidade adaptativa necessária à adaptação aos cenários actuais de alteração global.

Através da caracterização ecológica das espécies de ave amostradas foi também possível testar uma série de hipóteses relacionando a fisiologia das aves com a respectiva ecologia e comportamento. Várias teorias e hipóteses propostas na literatura a respeito de aspectos específicos da história de vida das aves foram também discutidas. Ficou também demonstrado que aparentes compromissos, entre várias características de história de vida, podem emergir a partir de constrangimentos metabólicos.

Os padrões observados para diversos parâmetros DEB, primários e secundários, foram significativamente explicados pelo tamanho do corpo. Factores como o tipo de desenvolvimento da cria, dentro do espectro altricial-precoce, ou a capacidade de voar ou migrar, foram também particularmente relevantes para este fim. Correlações positivas e fortes entre vários parâmetros DEB foram consistentes com a teoria da estratégia *waste-to-hurry*, com os custos de manutenção somática a aumentar em resposta a taxas mais elevadas de crescimento, determinando em última análise a evolução da condição altricial a partir de ancestrais precoces.

Foi também possível estimar que as crias de espécies precoces exibem valores mais elevados de maturidade por unidade de massa seca, quando nascem, do que as crias de espécies altriciais. Se considerarmos o investimento relativo em maturação como um indicador de complexidade, então estes resultados apoiam a tese de maior complexidade à nascença nas aves precoces.

Finalmente, o caso de estudo do Albatroz-errante (*Diomedea exulans*) é apresentado enquanto exemplo de como a disponibilidade de alimento pode determinar padrões de crescimento raros e extremos em ambientes particularmente limitados. A aplicação da teoria DEB permitiu o desenvolvimento de um modelo termodinamicamente explícito para esta espécie ameaçada, testando uma hipótese que explica o padrão de crescimento observado e providenciando outras propriedades metabólicas úteis, como a capacidade de jejum e o consumo energético diário das crias e dos adultos.

Palavras-chave

Aves; teoria *Dynamic Energy Budget* (DEB); conservação; evolução da história de vida; ciclo de vida; metabolismo; energia; estimação de parâmetros; Albatroz-errante; *Diomedea exulans*.

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